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The Effects of Sex, Energy, and Environmental Conditions on the Movement Ecology of Migratory Bats

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Graduate Program in Biology

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ABSTRACT

Lack of knowledge about the behaviour of migratory species during the migratory period is a major barrier to conservation efforts. In this thesis, I focus primarily on differences between the sexes of the bat *Lasionycteris noctivagans*, during spring migration. Females are pregnant during spring migration and this overlap between migration and reproduction may affect the time and energy management of females as compared to males. In Chapter 2, I examine spring migration phenology of bats at a stopover site. Females arrived earlier than males, likely to give their pups a long growing season. Fat stores appeared to reflect a strategy to provision for upcoming lactation demands. In Chapter 3, I explore stopover behaviour and I show that despite the use of torpor to minimize roosting energy expenditure, cold weather extends stopover duration. There was no sex difference in the length of time spent at stopover. By regressing the time of night bats were captured against their fat and lean mass I demonstrate that bats have greater fat and lean masses closer to dawn, and therefore are likely using stopover periods to refuel. In Chapter 4, I compare sex and seasonal differences in daytime torpor use at stopover. I found that in spring bats used torpor for fewer hours than in autumn, even after accounting for the effect of ambient temperature. Further, females used torpor for fewer hours than males. I propose that these seasonal differences are due to lower prey abundance and predictability in spring; sex differences may be attributable to a higher foraging intensity by females compared to males. Finally, in Chapter 5, I use a radio-telemetry array in southwestern Ontario, Canada to track the spring and autumn long distance migratory movements of *L. noctivagans*, *Lasiurus borealis*, and *Lasiurus cinereus*. No migration corridors were identified in either season. Estimated migration speeds indicate that multiday stopovers are also used in the autumn. These studies combined show that sex affects the spring migration time and energy management of bats. Bat migration research is still in its formative stages and my studies provide new information on bat migration in North America.

Keywords: automated radio-telemetry, body composition, Chiroptera, departure

decisions, energy balance, fat stores, flight behaviour, flight speed, heterothermy, *Lasionycteris noctivagans*, *Lasiurus borealis*, *Lasiurus cinereus*, leading lines, phenology, protogeny, migration, migratory corridor, migratory routes, migratory strategies, refueling, stopover, sex differences, tailwind assistance, thermoregulation, torpor, torpor-assisted migration, vernal migration, wind energy

STATEMENT OF CO-AUTHORSHIP

A version of Chapter 2 “Sex differences in spring migration timing and body composition of silvered-haired bats (*Lasionycteris noctivagans*)” was published in the *Journal of Mammalogy* with Christopher Guglielmo as co-author.

Chapter 3 “Evidence for spring stopover refueling in migrating silver-haired bats (*Lasionycteris noctivagans*)” will be submitted to the *Functional Ecology* with Christopher Guglielmo as co-author.

Chapter 4 “Cold Breaks: Seasonal and sex differences in daily torpor use by migrating silver-haired bats (*Lasionycteris noctivagans*)” will be submitted to *Physiological and Biochemical Zoology* with Christopher Guglielmo as co-author.

Chapter 5 “Spring and autumn migratory movements of North American Tree-bats (*L. noctivagans*, *L. borealis* and *L. cinereus*) using the MOTUS wildlife tracking system” will be submitted to *Animal Behaviour* with Christopher Guglielmo as co-author.

Chapters 2-5 are co-authored by Christopher Guglielmo. Dr. Guglielmo was involved in study design, provided equipment, assisted with interpreting the data and made editorial comments.

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CHAPTER 1

INTRODUCTION

1.1 WHY MIGRATE?

The annual movements of wildlife are one of the most conspicuous responses of animals to a seasonally variable world. Migration allows animals to respond to seasonality by avoiding energetic bottlenecks or taking advantage of peaks in resource abundance. For example, in North America many songbirds breed in the boreal forest to exploit the abundance of insects available in summer, but overwinter in the tropics to avoid harsh weather (Cox 1985). Other migrants move to use different habitat types for different stages of their life history. Baleen whales for example, migrate from polar feeding grounds to warmer waters for calving (Rasmussen et al. 2007). Bats fall into both of these categories, migrating seasonally to take advantage of food resources and to find suitable roost sites (see section 1.3.2).

A complex suite of traits is required to migrate successfully. Migrants must be able to correctly orient and navigate, arrive at their destination at appropriate times, and support increased exercise through physiological changes (Dingle 1996). Despite this complexity, migration has evolved in many taxa, including insects (e.g., aphids, butterflies, dragonflies), fish (e.g. eel, salmon, herring), reptiles (e.g. sea turtles), birds, and mammals (e.g. whales, caribou, bats) (Johnson 1954; Berthold 1993; Dragesund et al. 1997; Wassenaar and Hobson 1998; Corkeron and Connor 1999; Morbey 2000; Mahoney and Schaefer 2002; Fleming and Eby 2003; van Ginneken 2005; Wikelski et al. 2006; Sale and Luschi 2009). In order for migration to evolve, the benefits of movement must exceed the costs of transport and risks associated with occupying a new habitat (Alerstam et al. 2003). Thus, it is no surprise that taxa that migrate long distances have a relatively low cost of transport. Flight, while energetically expensive per unit time, has a lower cost of transport for a unit of distance than walking or running (Schmidt-Neilsen 1972). Bats are the only mammals capable of true flight, and in this way may be pre-adapted for

long distance migration. Bat species that migrate tend to have energetically efficient wings, which have high aspect ratios, high wing loading, and low wing tip indices (i.e. they are pointed) (Norberg and Rayner 1987).

1.2 SEX AND MIGRATION

The costs and benefits of migration do not always affect males and females equally. Differences between sexual selection pressures and morphology (e.g. body size) can shift the trade-offs made by migrants. These different selection pressures can lead to variation in migratory tendency and behaviour between sexes (Morbey and Ydenberg 2001; Chapman et al. 2011).

Partial migration is the phenomenon where only some members of a population migrate. Often the decision to migrate is dependent on trade-offs associated with body condition, age, or sex, such as differences in thermal tolerance, competitive ability, or fasting endurance (Chapman et al. 2011). For example, white-ruffed manakins (*Corapipo altera*) are small tropical birds that migrate between high-elevation breeding areas and low-elevation non-breeding areas. Male manakins are more likely to migrate downhill than females. This difference in migratory tendency is driven by body size; smaller bodied males are less tolerant of fasting during prolonged downpours at high altitudes, which limit their ability to forage and can result in starvation (Boyle 2008). Sexual selection pressures can also drive shifts in migratory tendency. Red-spotted newts (*Notophthalmus viridescens*) can either overwinter in ponds or migrate to terrestrial areas. In this species, females are more likely to develop the migrant phenotype. There is pressure for males to be at breeding ponds early in the spring to increase mating opportunities (i.e. residency)(Grayson and Wilbur 2009).

One frequent difference in migratory behaviour between sexes is a shift in the timing of movement. The most common pattern is protandry – the earlier arrival of males as compared to females. Protandrous arrival to breeding grounds is observed in many birds and salmonids, as early arrival confers a reproductive advantage to males competing for mates (Morbey and Ydenberg 2001). Early arrival can enhance male fitness by increasing

the number of mating opportunities, or because early arrivers secure the best breeding territories. Interestingly, in the sex-role reversed phalaropes (*Phalaropus spp.* – arctic breeding shorebirds) in which females compete for access to mates, the opposite pattern is seen – females arrive earlier than males, termed protogyny (Reynolds et al. 1986).

Sex differences in arrival on the breeding grounds are the product of changes in other migratory behaviours, such as departure timing, speed of migration, and latitudinal segregation on the wintering grounds. Migratory restlessness, or *Zugunruhe*, describes the behaviour of captive birds that are ready to migrate. There are innate sex differences in the onset of *Zugunruhe* in birds, with males becoming restless earlier in the season than females (Maggini and Bairlein 2012). This difference in the onset of *Zugunruhe* should result in earlier departure of males from the wintering grounds, as is seen in Hermit thrushes (*Catharus guttatus*) (Stouffer and Dwyer 2003). Male birds also may increase their speed of migration by refueling at faster rates than females (Seewagen et al. 2013). Finally, some birds may winter closer to their breeding grounds to facilitate earlier arrival. Latitudinal segregation on wintering grounds, with males wintering farther north than females, occurs in many temperate song birds (Komar et al. 2005), and is generally referred to as differential migration. Differential migration is when one demographic of a population (i.e. age or sex) migrates farther than another.

1.2.1 MIGRATORY SEX DIFFERENCES IN BATS

In bats migration tends to be female biased; females are both more likely to migrate and to move greater distances than males (Fleming and Eby 2003). This is the case for *Tadarida brasiliensis* (Wiederholt et al. 2013), *Nyctalus noctula* (Dechmann et al. 2014), *Nyctalus leisleri* (Ibáñez et al. 2009), *Lasiurus noctivagans*, and *Lasiurus cinereus* (Cryan 2003). Exceptions exist; male *Perimyotis subflavis* make longer latitudinal migrations than females (Fraser et al. 2012). Female bats have high energetic costs (associated with pregnancy and lactation), than males and females may benefit by traveling farther along a resource gradient than males (Fleming and Eby 2003). Further sexual segregation occurs because females must also seek roosts with warm, stable microclimates that are suitable for rearing their pups, while males seek cooler roosts to

save energy during torpor – a state of reduced metabolism and body temperature which confers substantial energy savings (Altringham and Senior 2005).

Temperate bats have an unusual reproductive timing compared to other mammals. Mating occurs in the autumn, but females store sperm in their reproductive tracts until the early spring when they ovulate and become pregnant (Crichton 2000). Thus, spring migration trade-offs may differ by sex because females are pregnant, while males have several months to prepare for autumn mating. This temporal mismatch in the timing of reproductive investment is likely to lead to sex differences in the timing of migration. Females are under selective pressure to give their pups a long growing season, as pups born earlier in the year are more likely to survive (Frick et al. 2010). Males, having mated the previous fall, are likely under selective pressure to move later in the spring when weather may be more hospitable. *Myotis lucifugus* females emerge from hibernation earlier than males, and thus begin migrating back to maternity colonies earlier (Norquay and Willis 2014). In preparation for the costs of reproduction, female *M. lucifugus*, manage their overwinter energy budget more conservatively than males. “Thrifty” females begin hibernation with larger energy stores and use them more slowly than males (Jonasson and Willis 2011). The same thrifty female strategy may also apply to the way that migrating bats manage their energy stores in anticipation of reproduction, but this question has not yet been investigated.

1.3 BAT MIGRATION

1.3.1 A brief history of bat migration research

The study of migration in bats has substantially lagged behind our understanding of bird and other animal migrations (Fleming and Eby 2003; Popa-Lisseanu and Voigt 2009). This is in part because the migrations of birds and other animals, such as insects, whales and sea turtles are far more prevalent and conspicuous.

In 1970, a comprehensive review examined the evidence that bats undertook migrations (Griffin 1970). This review summarized the occurrence records of bats that were likely migrants blown off course – those found on inhospitable coastlines, ships at sea, and on

islands where these species do not usually occur. Griffin (1970) also described the use of banded bat recoveries to infer migrations. Many of the first tracked movements of bats were discovered by intensive mark-recapture programs whereby unique bands were placed on the forearms, legs, or ears of bats roosting in hibernacula (hibernation sites) and individuals were later located at other hibernacula or maternity colonies (Griffin 1936; 1945; Davis and Hitchcock 1965). Major banding efforts of several Vespertilionids in Europe, *M. lucifugus* in the United States and *T. brasiliensis* in the southern United States and Mexico revealed the distances and directions of these migrations. For example, one *N. noctula*, a European species, was found to travel 1,125 km in 6 weeks. At this time the use of radio-transmitters was limited; transmitters weighed ~5 g and so could only be attached to very large bats without substantially affecting their behaviour (Griffin 1970).

A seminal review by Fleming and Eby (2003) covered in more detail which bat taxa migrate, expanding to include species from tropical regions and exploring the selection pressures that may have led to a migratory life history (see section 1.3.2). The authors explored some physiological consequences of migration, such as the deposition of fat to fuel movement, and estimated migration distances based on observed fat stores. Further, this review examined the population-genetics and social consequences of migration. As populations mix during migration, mating systems are unlikely to favor stable male-female associations in migratory species. Further, because migration is a relatively risky strategy compared to hibernation, it is expected that migrants will have higher levels of annual mortality and relatively fast life histories. Indeed many migratory species (*Pipistrellus. nathussi*, *N. noctula*, *Lasiurus spp*, and *L. noctivagans*) have litters of two pups a year as opposed to the one that is common in most species of bat. Fleming and Eby (2003) concluded with a comparison of the differences between the migratory ecology of birds and bats. The major difference they found was in life history timing; in bats there is a concurrence of pregnancy and spring migration, while birds mate after completing migration. The effect of bats unique reproductive timing on migration has received surprisingly little research since the time of this review.

More recently there has been increased interest in how bats undertake their migrations both physiologically and behaviourally, and exciting new work warranted a special edition of the *Journal of Mammalogy* (Popa-Lisseanu and Voigt 2009). A paper titled “What can birds tell us about the migration physiology of bats?” introduced the framework for physiological investigation of bats (McGuire and Guglielmo 2009), which was followed up by work investigating seasonal changes in migrant physiology. In migratory condition, *L. cinereus* decrease the size of digestive organs and increase the size of the heart and lungs (McGuire et al. 2013a). Further, migrating *L. cinereus* also upregulate fatty acid transporters and mitochondrial oxidative enzymes, necessary for high levels of fat metabolism during exercise (McGuire et al. 2013b). These changes demonstrate that migration poses distinct physiological challenges to bats.

The behaviour of migrating bats has also recently been explored in more depth. Acoustic detectors were used to monitor the airspace 100 m above the water to determine the direction bats flew along a river valley in Poland (Furmankiewicz and Kucharska 2009). The authors found bats moved predominantly north in the spring and south in the autumn, and concluded that these were migration flyways (Furmankiewicz and Kucharska 2009). Further evidence of relatively low altitude flight (e.g. < 500 m) during migration was found over the Baltic Sea, where bats flew close enough to remain in acoustic contact with the water (< 10 m) (Ahlén et al. 2009). Similarly, migrating *P. nathusii* on the shoreline of the Baltic coast of Latvia were observed flying within 16 m of the ground (Šuba 2014). The altitude at which most bats migrate remains unknown, as most observations of migration flight altitude have been opportunistic.

A major recent concern has been the high incidence of migratory bat mortality at wind energy facilities. Seasonal peaks in mortality at wind energy facilities occur during autumn migration (Arnett et al. 2008; Baerwald and Barclay 2009). Cryan and Barclay (2009) proposed numerous hypotheses to explain the causes of bat mortality at wind turbines, these fell into three categories: random collisions, coincidental collisions and collisions that are a consequence of attraction to these structures. Coincidental collisions place bats in the same airspace as turbines due to some aspect of their biology, while attraction collisions suggest that bats aggregate near turbines to investigate them out of

curiosity, to feed, roost, or seek mates (Cryan and Barclay 2009). Bats may not even need to collide with turbine blades to die, but may experience barotrauma due to low pressure at the vortices of turbine tips (Baerwald et al. 2008). Although there is contrasting evidence that most bats' injuries are more consistent with traumatic injury than barotrauma (Rollins et al. 2012).

1.3.2 Who Migrates?

Migration is relatively uncommon among bats. Less than 3% of bat species are known to migrate (Fleming and Eby 2003; Bisson et al. 2009), but perhaps more migrants will be revealed once they have received further study. The apparent low prevalence of migration in bats may be in part because most of bat diversity occurs in less seasonal tropical regions – only about 125 of the 1,300 species of bats reside in the Palearctic and Nearctic (Fleming and Eby 2003). Another reason that migration is less prevalent in bats than in birds is that in the face of dropping temperatures and low food abundance, many bats use daily torpor or hibernate, physiological responses that are very uncommon in birds (Geiser 1998). As compared to birds, the majority of bats undertake short migrations, usually less than 1000 km (Fleming and Eby 2003). Nevertheless, migration is an important aspect of some bat species life histories and occurs in nine out of seventeen families of bats (McGuire and Ratcliffe 2011). Within the largest family of bats, the Vespertilionidae, migration has evolved repeatedly, likely so that bats can seek appropriate winter roosts (Bisson et al. 2009). These migrations fall into regional, latitudinal, and altitudinal categories.

Regional migrations are movements in the direction of a specific resource, and the population's movement paths radiate out from this central resource. Many temperate vespertilionids in North America and Europe (e.g. *M. lucifugus*, *Myotis daubentonii*) undertake regional migrations, dispersing out from central hibernacula in spring and returning to them in autumn. These movements tend to be short (< 300 km), but some individuals can travel up to 500 km to reach suitable winter roosts (Fenton and Brockett 1970; Norquay et al. 2013). Other regional migrations include aggregations of 5 - 10 million straw-colored fruit bats (*Eidolon helvum*) that congregate in northern Zambia to

consume a seasonal pulse of fruit (Richter and Cumming 2005; 2008). Satellite-transmitter studies have shown that *E. helvum* is capable of moving up to 2000 km annually (Richter and Cumming 2008).

Latitudinal migrations involve movements that follow a climatic gradient, and therefore are usually farther than regional migrations. Large numbers of Brazilian free tailed bats (*T. brasiliensis*) migrate from Mexico to maternity colonies in the southern United States to meet the arrival of migratory moths (Bernardo and Cockrum 1962; Wiederholt et al. 2013). In Mexico, lesser long-nosed bats (*Leptonycteris yerbabuenae*) undertake latitudinal migrations of several hundred kilometers to follow the development of a “nectar corridor” as cacti come into bloom (Rojas Martínez et al. 2009).

Altitudinal migrations are those up or down an elevational gradient, and similar to latitudinal migrations, bats are moving between climatic zones. *Miniopterus natalensis* undertake migrations up Mount Kilimanjaro to seek cold hibernacula (Voigt et al. 2013). Altitudinal migration may be more common in bats than currently appreciated, and this phenomenon deserves further investigation (McGuire and Boyle 2013).

1.3.3 Tree-bat Migration

“Tree-bats” is a general term for those species that roost almost exclusively in foliage, under loose bark or in tree cavities. “Cave-bats” are species dependent on caves for some period of the year. Several species of North American tree-bats (*Lasiurus cinereus*, *Lasiurus borealis*, and *Lasionycteris noctivagans*) are thought to make latitudinal migrations, similar to birds, traveling south for the winter. As these tree-bats are solitary, their movements are more difficult to observe than those of species which form large aggregations. Several lines of evidence support the theory of tree-bat migration. The first were chance observations of bats that had collided with a lighthouse, found while searching for migrating birds that had also struck the lighthouse (Saunders 1930). At another bird observatory on a remote island 32 km offshore from Point Reyes California, the appearance and disappearance of *L. cinereus* roosting in trees was correlated with low winds and low moon illumination (Cryan and Brown 2007). Cryan (2003) mapped the

localities of museum specimens and described seasonal shifts in occurrence of tree bats – an expansion northeastwards in the summer, with females traveling further than males. Stable isotope analysis of bat fur can reveal the general area in which the fur was grown and can be used to infer movement when bats are found at sites away from the locality where molting occurred. Several studies of bat fur have shown support for latitudinal movements (Cryan et al. 2004; Fraser 2011; Voigt et al. 2012; Baerwald et al. 2014). Acoustic monitoring detects the echolocation calls of bats, and can be used to passively monitor bat activity. This technique has been used to document the seasonal increase in bat activity associated with migration (Baerwald and Barclay 2009; Hamilton 2012). Higher levels of acoustic activity at sites closer to the Rocky Mountains has been noted in support of the hypothesis that bats use linear landscape features to guide migratory routes (Baerwald and Barclay 2009). Most recently, miniaturized Global Positioning System (GPS) tags were used to record a handful of localities that male *L. cinereus* in California used throughout the year (Weller et al. 2016).

Tree-roosting bats are hypothesized to move to milder climates to find hibernacula that will buffer them against the winter conditions (Fleming and Eby 2003). Therefore it is not surprising that long distance, latitudinal migration has been more likely to evolve in tree-roosting bats, than those that use caves or buildings (which offer a stable microclimate, even in harsh winter conditions) (Bisson et al. 2009).

The ecology of North America's migratory, tree-roosting bats is still largely unknown, and even less is understood about the behaviour and habitat requirements of these species during migratory periods (Cryan and Veilleux 2007). Migration is presumed to be energetically demanding and a period of increased mortality for bats (Fleming and Eby 2003). Yet, little is known about how tree-bats acquire and manage their energy stores during migration, and how these factors shape movement patterns. There remain questions as to how individual attributes (e.g. sex and energetic state) affect how migrating bats manage their energy stores and virtually nothing is known about how bats amass fuel stores to support migration. For example, we do not know if bats forage *en route*, or carry sufficient fat stores to complete migration with little or no feeding. Similarly, recent work using isotope analysis has provided insights regarding the broad

movement patterns of populations (Cryan et al. 2004; Fraser et al. 2012; Voigt et al. 2012; Baerwald et al. 2014), however, questions regarding the movements of individuals, and how traits such as sex and energy stores affect movement remain largely unexplored.

1.4 STUDY SPECIES

Lasionycteris noctivagans (LeConte, 1831), the silver-haired bat (Fig. 1), is a small (8-15 g) aerial hawking insectivorous species in the family Vespertilionidae (Kunz 1982). It is widely distributed from southeastern Alaska, across the southern half of Canada, and into the southern United States.

Acoustic surveys show that Long Point, Ontario, a world renowned stopover site (a place for rest and refuel between flights) for migratory birds is a promising site for migratory *L. noctivagans* research in the August and September (Dzal et al. 2009). This site was subsequently used to conduct the first study of migratory bat stopover; McGuire et al. (2011) found that *L. noctivagans* stop only briefly (~ 1 day) compared to bird species migrating through the same site (3 - 7 days). To explain the very short stopover duration of bats they proposed the “torpor-assisted migration hypothesis”. Bats, unlike most birds, can use daily torpor to drastically reduce the cost of thermoregulation during non-flight periods. Therefore, if migrating bats use daily torpor they would require much less time to refuel, or may not refuel at all. McGuire, Guglielmo and I returned to Long Point in 2011 and found strong support for the torpor assisted migration hypothesis using temperature-sensitive radio-telemetry. Both sexes of *L. noctivagans* readily entered torpor during the day, and the extent of torpor use was dependent on ambient temperature (McGuire et al. 2014).



FIG 1.1– A silver-haired bat equipped with a radio-transmitter and identifying lipped forearm band (arrows). This rare polydactylus individual has an extra thumb on each wing (circled) and an extra toe on each foot.

Mating in tree-bats likely coincides with the autumn migration period (August – September), when males are in a state of mating readiness as shown by development of keratinized spines on the glans penis and have sperm in the caudae epididymis (Druecker 1972; Cryan et al. 2012). *L. noctivagans* overwintering sites have also been challenging to locate, in part because this species does not form large colonies, unlike many cave hibernating bat species (Kunz 1982). *L. noctivagans* winter range extends throughout the southern United States (Izor 1979). One study found a small population overwintering solitarily or in groups of 2 - 3 under the bark of live, mature trees in Arkansas (Perry et al. 2010).

In the early spring, shortly after emergence from presumed hibernation, females ovulate and eggs are fertilized with sperm stored since the autumn (Druecker 1972). Locations for capturing spring migrants have also been challenging to locate. Delta Marsh (southern Manitoba, Canada) was known as a possible spring stopover site, but the roosting habitat was destroyed by a flood in 2011. A study at Delta Marsh of migrating individuals characterized roost selection, finding that bats preferred older trees with furrowed bark (Barclay et al. 1988). This study also demonstrated that migrant *L. noctivagans* entered torpor while roosting in the April and May, with some individuals remaining in roosts for several days when environmental temperatures were cold.

L. noctivagans usually give birth to twins in mid-June after an estimated 50 - 60 day gestation period followed by a 36 day lactation period (Druecker 1972; Kunz 1982). From June through August, *L. noctivagans* roost solitarily or form small maternity colonies of approximately 10 - 55 individuals in trees under loose bark, crevices, or cavities (Kunz 1982; Mattson et al. 1996).

1.5 METHODS FOR TRACKING SMALL MIGRANTS

Migration, by its very nature is logistically challenging to study. Migration of tree-bats is particularly difficult to study because of their elusive nature and small body size. Bat migration research has been hindered by the “small animal problem,” that is, technology small enough to attach to animals weighing < 190 g, has only recently become available

(Holland and Wikelski 2009; Bridge et al. 2011). It is generally widely accepted that in order to not substantially affect the behaviour or survival of flying animals, technology exceeding 5 % of body mass should not be affixed (Aldridge and Brigham 1988).

GPS tags are now as light as 1 g, which allows attachment to the very largest of the tree-bat – *L. cinereus* (body mass 25 - 30 g). However, a major limitation of this technology is that the bat must be recaptured for the data to be downloaded, and recordings are limited to a handful of GPS fixes at predetermined times. Light level geolocators, although light weight (0.5 g), are still too large for the smaller species of bats. Further, geolocators rely on the timing of sunrise and sunset to determine location, they are therefore are not useful for study of nocturnal species that spend the day roosting in shade (Lisovski et al. 2012).

Radio-transmitters are one of the lightest tracking technologies available (< 0.5 g). Transmitters broadcast a radio signal that can be detected for a few hundred meters or a few kilometers. In some cases migrating individuals can be tracked by small aircraft e.g. (Wikelski et al. 2003; Dechmann et al. 2014). This method is labor intensive, and a limited number of subjects can be tracked concurrently. Tracking by plane often relies on finding bats the day after they have completed their migratory flight, rather than tracking them in real time.

The Motus wildlife tracking system is a radio-telemetry array, comprised of > 150 towers in North America, and specifically concentrated in southwestern Ontario and the east coast of Canada. Rather than chasing individuals with a single receiver, the Motus array is a mesh of “checkpoints” across the landscape that animals fly past. All radio receivers monitor a single radio frequency, and tags on animals broadcast a unique identifying pulse signature. This technology represents an exceptional opportunity to track the movements in real time of small-bodied migrants. I used Motus to track the movements of migrating bats for the first time.

1.6 THESIS OBJECTIVES

My thesis examines differences in tactics used by male and female silver-haired bats (*L. noctivagans*) during spring and autumn migration – their movement ecology. Movement ecology encompasses the study of the causes, mechanisms, and patterns of movement as well as their consequences (Nathan et al 2008). It is currently unknown how season affects the migration strategies of bats. Spring and autumn migrations present different challenges both in terms of environmental conditions and life history selection pressures that drive individual behaviours. It follows that migrants often employ different strategies, shifting the importance of time or energy conservation, during different migration seasons. Spring migration is interesting because cold weather places an energy constraint on food acquisition (fewer insects are airborne at low temperatures). Further, female bats are pregnant during their northward migration (see section 1.2.1). Only two bat migration studies have been conducted in the spring. One was a roost selection study (Barclay et al. 1988). The other found sex differences in the thermoregulation of captive *L. cinereus* – females were less likely to enter torpor than males (Cryan and Wolf 2003).

The objectives of this thesis were three-fold: 1) To investigate spring migration, specifically how sex affects the passage timing though, and use of refueling habitats. 2) To further explore the torpor-assisted migration hypothesis in the spring, when females may avoid torpor. 3) To use Motus to track the long-distance movements of migrating bats during both spring and autumn.

1.7 THESIS STRUCTURE

This thesis is structured as a series of integrated articles that will each be published separately. These chapters examine how bats manage their time and energy on different temporal and geographic scales. I focus on how sex and season affect the ways that the currencies of time and energy are expended.

In Chapter 2, “Sex differences in spring migration timing and body composition of silver-haired bats *Lasionycteris noctivagans*” I examine the spring migration timing of bats.

Phenology describes the annual timing of events such as emergence from hibernacula, and arrival of migrants, and how these phenomena relate to climate. I hypothesized that the selective advantages for females to reach summering grounds early to raise their pups would result in protogyny, the earlier arrival of female as compared to male bats. My second objective was to determine how fat stores relate to arrival timing. If earlier bats have larger fat stores, it may provide “insurance” against inclement weather, or alternately the “reproductive hypothesis” suggests that females have larger fat stores as compared to males to help them fuel pregnancy and lactation after completing migration. I test the predictions of both the “insurance” and “reproductive” hypotheses.

Chapter 3, “Evidence for spring stopover refueling in migrating silver-haired bats *Lasionycteris noctivagans*” investigates the migration strategy of bats. It has been suggested that autumn migrating silver-haired bats have sufficient energy stores, such that they may not need to spend prolonged periods refueling (i.e. torpor-assisted migration)(McGuire et al. 2011), or that bats are able to meet their energy needs by foraging on the wing (i.e. fly-and-forage migration)(Šuba et al. 2012). Studies on migration refueling have taken place in the autumn, when prey are abundant, but this has not been examined in the spring when prey densities may warrant a different refueling strategy. I used a radio telemetry array to determine how long bats remain in the Long Point, Ontario region after first capture. Further, we examined the fat and lean mass of bats captured throughout the night to determine if they were gaining mass at our study site, as would be expected if Long Point was being used as a stopover refueling site.

Chapter 4, “Cold breaks: seasonal and sex differences in torpor use of migrating silver-haired bats *Lasionycteris noctivagans*” explores thermoregulation patterns of migrating bats and their relation to overall energy balance. The cost of thermoregulation is high for small endotherms (i.e. birds and mammals) because their high surface area to volume ratio increases heat loss to the environment. Torpor is a suite of adaptations that can result in substantial energy savings for small bodied animals. Torpor is a state of depressed metabolic rate and lowered body temperature that decreases heat loss to the environment (Geiser 2004). Bats are well known for their extensive use of torpor, but

only two studies have explored its use during the migratory period (Cryan and Wolf 2003; McGuire et al. 2014). Energy expenditure during non-flight periods is a substantial factor for birds, accounting for 70% of the migration energy budget (Wikelski et al. 2003), but bats may manage this cost differently. The aim of this chapter was to examine how free-ranging bats use torpor during spring as compared to autumn migration, and examine the effects of fat stores and sex on torpor expression.

In Chapter 5, “Spring and autumn migratory movements of North American Tree-bats (*L. noctivagans*, *L. borealis* and *L. cinereus*) using the Motus wildlife tracking system” I used a new radio-telemetry array to track the movements of individual bats as they traversed south-western Ontario. I hypothesized that bats follow leading lines, such as the shorelines of the Great Lakes or the Niagara escarpment while migrating. This has been proposed based on acoustic data (Baerwald and Barclay 2009; Furmankiewicz and Kucharska 2009), but not demonstrated by tracking the paths of individuals. The second objective was to quantify overall migration speed and, if possible, migration flight speed, which will give insights into bat migratory behaviour, and potentially how bats allocate their time to refuel versus making migratory movements.

I conclude my thesis with Chapter 6 in which I summarize and integrate my general findings, as well as propose future directions for bat migration research.

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CHAPTER 2

SEX DIFFERENCES IN SPRING MIGRATION TIMING AND BODY COMPOSITION OF SILVERED-HAIRED BATS *LASIONYCTERIS NOCTIVAGANS*¹

2.1 ABSTRACT

Early arrival on the summering grounds with ample energy stores may give a fitness advantage to females preparing to raise pups. In contrast there is no such fitness gain for males because they invest in mating during autumn. I use three years of capture data to investigate sex differences in spring migration passage date and body composition of *Lasionycteris noctivagans*. I predicted that females would arrive earlier in the spring and maintain greater fat stores than males. Females passed through the study site earlier and had more fat than males in two of three study years. Cold weather appeared to delay female migration and to deplete fat stores, but did not appear to affect the passage date or fat stores of males. My findings indicate that sex differences occur in the timing and energy management of bats during spring migration. I postulate this difference in migration strategy is related to the increased demands of reproduction once females arrive at their summering grounds. My results also suggest that females fuel migration with energy acquired *en route* to a greater extent than males.

Key words: Chiroptera, fat stores, phenology, protogyny, migrate, vernal migration

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2.2 INTRODUCTION

Migration evolves in response to predictable shifts in resource availability (Dingle 1996). Initiation of migration and the pace of movement must be coordinated such that arrival matches the development of resources at the destination (Jones and Cresswell 2010). Species and population-level timing of bat migration has been documented at several sites in North America and Europe using acoustic detectors (Baerwald and Barclay 2009; Furmankiewicz and Kucharska 2009; Rydell et al. 2014). Still, little is known about how individual bats migrate or sex differences in timing of movements by migratory bats, particularly the North American tree-bats (genera *Lasiurus* and *Lasionycteris*).

When the consequences of early or late arrival are contingent on traits such as sex, life history stage, or body condition, differential selection on migration timing may result. Notable examples are the protandrous migrations of many passerine birds (Francis and Cooke 1986; Spina et al. 1996; Rubolini et al. 2004) and salmon (Morbey 2000) – male migrants arrive earlier than females. Natural selection can act directly on the timing of males relative to females, or indirectly result in the arrival of one sex before the other, based on traits associated with sex (Morbey and Ydenberg 2001). Direct selection on males to maximize their mating opportunities has likely contributed to the evolution of protandry in pacific salmon (Morbey 2000). Similarly, highly polygynous bird species, which have greater male-male competition, also show a greater degree of protandry (Rubolini et al. 2004; Coppack et al. 2006). In contrast, indirect selection occurs when the costs and benefits differ for each sex, but not in reference to each other's timing. For example, the “weather sensitivity hypothesis” predicts that migration timing will differ if one sex is more vulnerable to environmental conditions than the other (Conradt et al. 2000). Such is the case in Great bustards (*Otis tarda*), which are sexually dimorphic. The larger bodied males are less tolerant of warm temperatures and migrate earlier than females to avoid extreme summer heat (Palacín et al. 2009).

The timing of tree-bat migration is likely driven by the temporal mismatch of male and female reproductive investment. Temperate zone bats usually begin mating in the autumn and exhibit delayed fertilization – females ovulate in the early spring and fertilize eggs

with sperm stored from autumn mating (Entwistle and Racey 2000). Female migration timing is more likely to reflect costs and benefits of raising pups. Arrival at the breeding grounds must be timed to match the development of resources in the spring, and fall timing may be constrained by the time needed to prepare for migration after weaning young. Whereas male migration timing is likely influenced by mating activity in autumn. Males may be positioning themselves to intercept the greatest number of females, similar to the prolonged swarming season of males in hibernating bat species (Burns and Broders 2015). Consistent with the hypothesis that *L. noctivagans* mates along the migration route, the passage timing of adult male and female autumn migrants coincided at a wind energy facility in southern Alberta, Canada (Baerwald and Barclay 2011). Here I present a three-year study to test the hypothesis that the timing of spring migration and body condition differ between sexes in *L. noctivagans*. I made the following predictions.

Prediction 1.—*Lasionycteris noctivagans* are protogynous – females will pass through the stopover site earlier in the season than males. Early arrival on the summering grounds should give females, but not males, a fitness advantage. For example, early-born pups are more likely to survive their first winter and reproduce as yearlings, as is shown in the hibernating species *Myotis lucifugus* and *Eptesicus fuscus* (Frick et al. 2010; Barclay 2012). Further, *M. shreberi* and *M. lucifugus* females emerge from hibernation earlier than males (Rodrigues and Palmeirim 2008; Norquay and Willis 2014), likely because this facilitates earlier parturition (Racey 1976). I expect a similar phenology in migratory species, as *L. noctivagans* females would also benefit by arriving on the summering grounds early. In contrast, there should be no reproductive incentive for males, which mated the previous autumn and do not provide parental care, to time their spring migration in reference to females or to move while environmental conditions are marginal. Thus, I expect females migrate earlier in the spring than males.

Prediction 2.—Females will have larger fat stores than males. If female bats are protogynous, then according to the “insurance hypothesis” (Sandberg & Moore 1996), “overloading” fat may be valuable to safeguard against inclement weather encountered early in the season. If fat is used as insurance, then it would be expected that early

arrivers that are likely to face harsher conditions and have larger fat stores than those arriving later in the season. Alternately, the “reproductive hypothesis” posits that fat “left over” following migration is needed during pregnancy or lactation. Arrival on the breeding grounds with large energy stores has a positive effect on reproductive fitness of migratory birds (Sandberg and Moore 1996). This benefit is seen even in income breeders that “pay” for reproduction with resources accumulated on the breeding grounds (Smith and Moore 2003). Ample fat stores in the spring likely provide such a benefit to female bats which face high energy demands during lactation (Kurta et al. 1989).

2.3 MATERIALS AND METHODS

2.3.1 Study Species

Lasionycteris noctivagans (LeConte 1831) is a small (8-14 g) insectivorous species of the family Vespertilionidae (Kunz 1982). This species is widely distributed from southeastern Alaska, across the southern half of Canada, and into the southern United States. Evidence for migration in this species comes primarily from seasonal peaks in occurrence records and stable isotopes (Cryan 2003; Baerwald et al. 2014). *Lasionycteris noctivagans* reproductive life history overlaps with migratory periods; both sexes are in a state of mating readiness during autumn migration (Cryan et al. 2012) and females are pregnant during their spring migration, although the stage of embryonic development is uncertain (Druecker 1972). After an estimated 50-60 day gestation period females usually give birth to twins in mid-June (Druecker 1972; Kunz 1982). During the summer, *L. noctivagans* roost solitarily or form small maternity colonies of approximately 10-55 individuals in trees under loose bark, crevices, or cavities (Kunz 1982; Mattson et al. 1996). During migration, bats roost solitarily and use similar types of tree roosts (Barclay et al. 1988). Overwintering ecology of this species is poorly known, bats are hypothesized to use multi-day torpor (hibernation) and leave roost sites to drink or forage opportunistically (Cryan and Veilleux 2007; Perry et al. 2010).

2.3.2 Study site and capture methods

I conducted my study at the base of Long Point, a narrow 35 km long sand peninsula projecting southeast from the north shore of Lake Erie, Ontario, Canada (42°34'N, 80°20'W). The study site is located just north of the center of the annual distribution of *L. noctivagans*. This region is a renowned stopover site for migratory birds, and prior to my study Long Point had also been identified as an important site for migrating bats in the autumn (Dzal et al. 2009). I captured bats at the Old Cut field station of the Long Point Bird Observatory during the spring migration period in 2012 - 2014 (April 3-May 31, 2012; April 14-May 27, 2013; April 4-June 5, 2014). The netting site was a 9-ha woodlot, comprised of mixed conifers and deciduous trees, adjacent to a marsh and residential development (year-round and seasonal cottages). Mist-nets ranging from 3 – 7 m in height, were opened from dusk until dawn every night unless this was prevented by rain, high winds, or ambient temperatures (T_a) below 3 °C (no bats were captured below 5 °C in the first year of the study). I measured body mass ± 0.1 g using a digital scale (CS200, OHAUS, Parsippany, NJ, USA), forearm length (mm) as an indicator of body size, and body composition for each bat. Body composition was measured using quantitative magnetic resonance (QMR, EchoMRI-B; Echo Medical Systems, Houston, TX, USA), a non-invasive method that measures wet lean mass (g) $\pm 2\%$ and dry fat mass (g) $\pm 10\%$ without the use of anesthetic or restraint (McGuire and Guglielmo 2010). QMR measurements took place in a field laboratory. Bats were placed in a 3 cm diameter ventilated plastic tube which was then inserted into the QMR machine for two replicate two minute scans (additional details in McGuire et al. 2010). The magnetic field generated by the QMR does not interfere with the orientation abilities of *L. noctivagans* (McGuire et al. 2011). Female bats were palpated to feel for a fetus, but none were detectable. Hourly temperature recordings (± 0.1 °C) were obtained from a weather station at Bird Studies Canada headquarters in Port Rowan (6 km from the capture site). All research activities were approved by an Animal Use Protocol from the University of Western Ontario Council on Animal Care (protocol 2010-020; Appendix D), and were permitted under a Wildlife Scientific Collector's Authorizations from the Ontario Ministry of Natural Resources (authorization no. 1067554, 1073065 and 1076439; Appendix E).

2.3.3 Analyses

Passage Timing. First capture date was used as an indicator of arrival at the stopover site. I used a two-way analysis of variance (ANOVA) to examine capture date at my site using the predictor variables of sex and year, and the interaction sex \times year. Tukey tests were then used to examine how capture date was influenced by sex within years, and were also used to examine between year differences for males and females separately.

To test the prediction of the “insurance hypothesis” that bats which have greater fat stores are able to arrive earlier in the migration season, I investigated the effect of fat mass on capture date using a general linear model. I used data from bats captured in 2012 and 2014, when I was able to measure body composition for the entire season. In 2013, the QMR was only available for use in the month of April. This model for capture date included sex, year, the interaction sex \times year, as well as fat mass and a measure of body size (forearm length). The effect of T_a among the three study years on annual mean values of capture dates for males and females was examined using simple linear regressions. To do this I averaged hourly recordings taken during the spring migration capture period (April and May combined).

Body Composition. Three measures of body composition (fat mass, percent body fat and wet lean mass) were investigated using general linear models and the predictor variables sex, year, sex \times year, and forearm length as a measure of body size. I tested for a correlation between fat mass and forearm length using simple linear regression. Finally, the effect of ambient temperature (T_a) among the three study years on annual mean values of fat mass for males and females was examined using simple linear regressions.

All values are reported as mean \pm SD. Significance was assessed at an α of 0.05 and models used type III SS. Statistical analyses were conducted in the program R (version 3.0.2; R Development Core Team 2009).

2.4 RESULTS

2.4.1 Passage timing

The first bats were captured between April 14 -16 in all three years. Capture date was affected by the interaction of sex \times year ($F_{2,108} = 15.4$, $P < 0.001$), year ($F_{2,108} = 12.5$, $P < 0.001$), and sex ($F_{1,108} = 48.5$, $P < 0.001$; full model $F_{5,108} = 21.1$, $P < 0.001$). Mean female capture date was 30 days earlier than male capture date in 2012 ($P < 0.001$) and 14 days earlier in 2014 ($P < 0.001$), there was no sex difference in capture date in 2013 ($P = 0.99$; Fig. 2.1). Females arrived incrementally later over the three years of the study, but there was only a significant difference between female arrival in 2012 and 2014 ($P < 0.001$). Males arrived earlier in 2013 as compared to both 2012 and 2014 ($P < 0.001$). The total passage timing (days between first and last capture) of females was longer than males in 2012 and 2014, but was comparable in 2013 (Table 2.1).

Using data from 2012 and 2014 (when it was possible to take QMR measurements of all bats), I examined the effect of fat on passage timing. After year and sex effects were accounted for, inclusion of fat mass ($P = 0.17$) and forearm length ($P = 0.47$) did not significantly contribute to the model for capture date ($F_{5,54} = 29.7$, $P < 0.001$). Greater fat mass was not associated with earlier arrival dates in either sex.

Females arrived earliest in the warmest years – mean capture date was negatively correlated with mean spring migration T_a (Fig. 2.2A; $R^2 = 0.99$, $P = 0.04$). There was no effect of mean spring migration T_a on mean capture date of males (Fig. 2.2A; $P = 0.94$). Cooler T_a were associated with wider migration windows in females, but not males (Table 2.1).

Table 2.1– Number of nights between 1st and last capture of male and female *L. noctivagans* migrating through Long Point, Canada in the spring.

Year	Sampling period length (days)	Males (days)	Females (days)	Mean migration season T_a at capture site ($^{\circ}\text{C}$)
2012	59	8	23	12.0 ± 6.4
2013	45	36	36	10.6 ± 6.9
2014	63	23	47	9.7 ± 5.8

Table 2.2– Body composition of spring migrating *L. noctivagans* measured using quantitative magnetic resonance

Year	Sex	<i>N</i>	Wet lean mass (g)		Fat mass (g)		Fat (%)	
			Mean \pm <i>SD</i>	Range	Mean \pm <i>SD</i>	Range	Mean \pm <i>SD</i>	Range
2012	M	8	8.24 ± 0.48	7.45-8.83	1.15 ± 0.42	0.55-1.71	10.7 ± 3.1	6.2-14.6
	F	16	8.92 ± 0.74	7.85-10.23	2.08 ± 0.70	1.03-3.33	16.6 ± 4.6	8.7-22.8
2013	M	7	7.72 ± 0.41	7.45-8.65	0.56 ± 0.13	0.36-0.70	5.7 ± 1.2	6.8-3.9
	F	16	8.35 ± 0.69	7.10-9.22	1.26 ± 0.63	0.34-2.64	11.1 ± 4.6	3.4-19.4
2014	M	15	8.16 ± 0.57	6.98-9.04	0.97 ± 0.31	0.36-1.41	9.2 ± 2.4	4.1-11.9
	F	22	8.80 ± 0.55	7.91-9.96	1.13 ± 0.40	0.47-2.02	9.9 ± 3.0	4.6-16.4

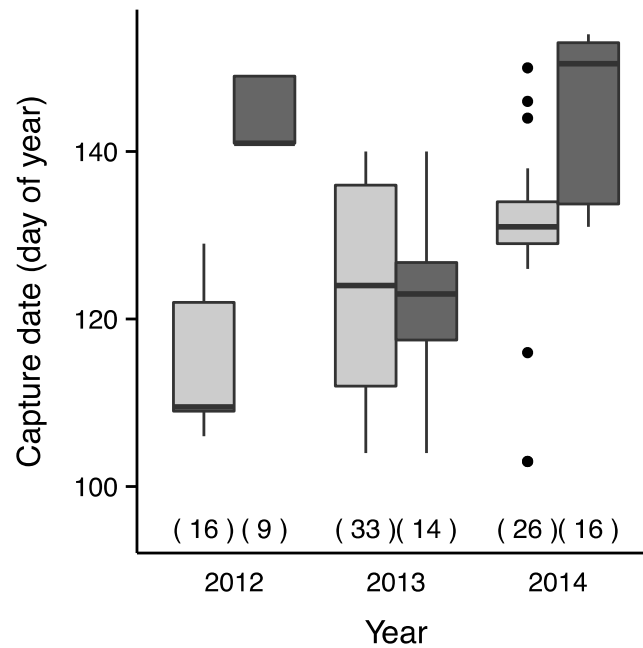


FIG. 2.1—Timing of spring migrating *Lasionycteris noctivagans* at a stopover site Long Point, Canada (day of year 120 = May 1). Female silver-haired bats (light boxes) were captured significantly earlier than males (dark boxes) in 2012 and 2014. In 2013 the lack of difference appears to be driven by early arrival of males as compared to other years. Distribution of data is shown using Tukey's box plots. Boxes designate the interquartile range, between the first and third quartiles and containing 50% of the observations, and are divided by the median. Whiskers connect boxes to the extreme points within 1.5x the interquartile range and points outside this range are individually plotted. Sample sizes are indicated in brackets below.

2.4.2 Body composition

Female *L. noctivagans* were 1.8% larger (forearm length: $t_{68} = 3.3$, $P = 0.001$; female = 41.8 ± 1.1 mm, male = 41.0 ± 1.2 mm) and 11.3% heavier than males (body mass: $t_{90} = 6.5$, $P < 0.001$; female = 11.5 ± 1.2 g, male = 10.2 ± 0.9 g). Absolute fat mass was affected by the interaction of sex \times year ($F_{2,76} = 4.1$, $P = 0.02$), year ($F_{2,76} = 18.4$, $P < 0.001$), and sex ($F_{1,76} = 17.1$, $P < 0.001$; full model $F_{5,76} = 10.8$, $P < 0.001$). Forearm length was not correlated with absolute fat mass ($P = 0.05$). Percent body fat showed the same relationship as absolute fat (full model $F_{5,76} = 10.3$, $P < 0.001$). Forearm length was not a significant factor in the absolute fat ($P = 0.52$) or percent fat mass models ($P = 0.79$). Females had larger absolute fat stores than males in 2012 ($P < 0.001$) and 2013 ($P = 0.03$), but there was no sex difference in 2014 ($P = 0.93$; Table 2.2; Fig. 2.3A). Wet lean mass was predicted by forearm length ($F_{2,76} = 12.4$, $P < 0.001$) sex ($F_{1,76} = 5.4$, $P = 0.02$) and year ($F_{2,76} = 4.8$, $P = 0.01$; full model $F_{6,76} = 8.6$, $P < 0.001$). Females had greater wet lean mass than males (Table 2.2; Fig. 2.3B).

Annual variation in mean absolute fat mass was not significantly correlated with spring migration T_a in either sex (Fig. 2.2B; $P > 0.05$). There was a tendency for female mean fat mass to decline with T_a , however three years of data were not sufficient to fully test this relationship.

2.5 DISCUSSION

My findings suggest that male and female *L. noctivagans* have different migration strategies in the spring. Consistent with my prediction of protogyny, the passage date of females was earlier than males in two of three years, and median passage date of males never preceded that of females. My second prediction was also partially met; after accounting for larger female body size, female bats carried fat stores that were nearly two times larger than those of males in two out of three study years. My three-year data set did not allow me to rigorously test which factors drive annual variation in passage date and body composition, however, the direction of these trends is noteworthy, and they should guide future studies.

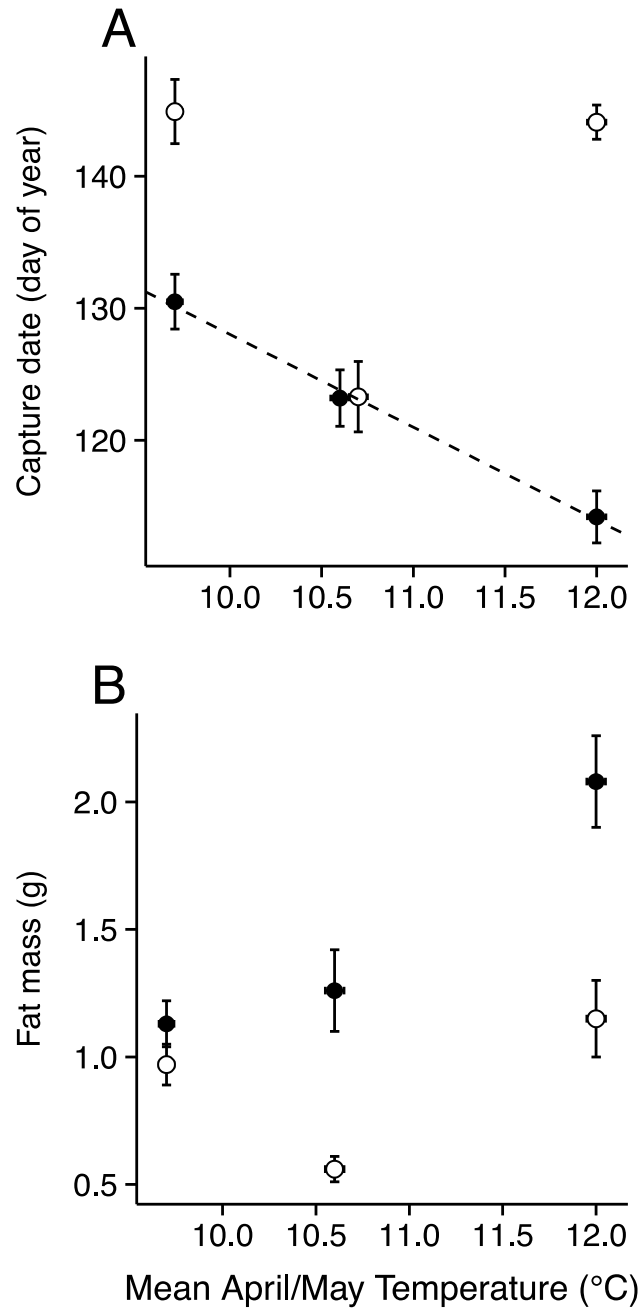


FIG. 2.2—The effect of T_a on spring migrating *Lasionycteris noctivagans*. Temperatures were 12.0, 10.6, and 9.7 $^{\circ}\text{C}$ in 2012–2014, respectively. A) capture date – females (closed circles) passage date advanced with warmer T_a , while no relationship was seen in males (open circles); B) fat mass – female fat mass declined with T_a , although not linearly. X and Y error bars denote SE. The data point for males in 2012 has been shifted 0.1 $^{\circ}\text{C}$ in panel A, so that it is visible.

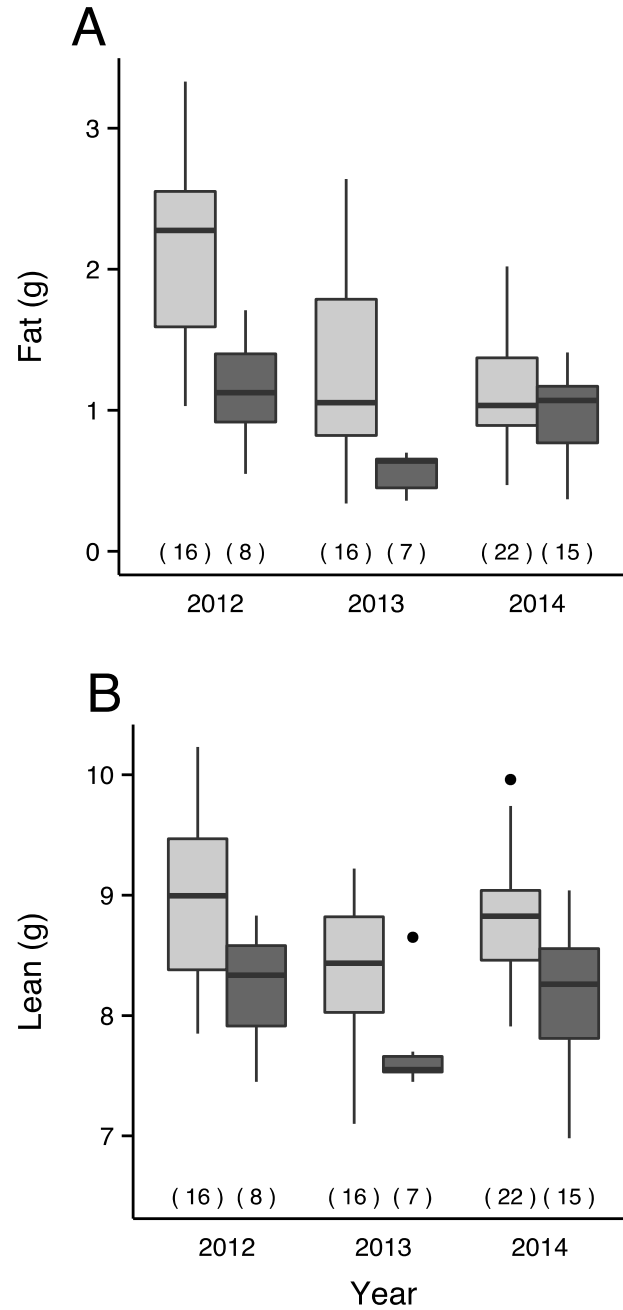


FIG. 2.3—Body composition of spring migrating *Lasionycteris noctivagans* captured at a stopover site Long Point, Canada. A) Females (light boxes) had significantly greater absolute fat mass than males (dark boxes) in during spring migration in 2012, and 2013, but not 2014. B) Wet lean mass of females was greater than males in all years.

2.5.1 Passage timing

Earlier spring arrival likely confers a reproductive advantage for female bats. Early birth increases survival of *M. lucifugus* and *E. fuscus* pups by allowing them more time to grow and accumulate fat before hibernation (Frick et al. 2010; Barclay 2012). Young *L. noctivagans* may realize a similar benefit by having additional time to prepare for their first migration. Early arrival on the breeding grounds is associated with increased fledging success in several taxa of migratory birds, including warblers (American redstarts; Smith and Moore 2005), raptors (black kites; Sergio et al. 2007), and seabirds (cormorants; Gienapp and Bregnballe 2012).

Years when female *L. noctivagans* arrived late corresponded with cooler spring temperatures at the capture site. This delay was also reflected in the longer total migration windows of females in colder years. Low T_a delays arrival to breeding grounds of aerial insectivorous birds, such as swallows (*Hirundo rustica*; Sparks 1999). A study of 15 bird species at my study site (Long Point, ON) revealed that for every 1 °C increase in mean spring migration T_a , the mean passage date of migratory birds advanced by one day (Marra et al. 2004). On average, mean female *L. noctivagans* capture date advanced by eight days for every 1 °C increase in mean spring migration T_a . This rate should be treated with caution because it was calculated using only three years of data. Nonetheless, the relationship between T_a and female passage date is informative, and it suggests that female bats face analogous limitations to birds during their spring migration. The migration pace of birds is largely determined by periods of stopover, where models predict that 7-fold more time is spent refueling than in migratory flight (Hedenstrom and Alerstam 1997). Poor weather can limit foraging opportunities particularly for insectivores because the rate of arthropod development depends on T_a (Lee 1991). I hypothesize that the delay of female bats observed in cold years could be in part due to refueling limitations.

The second way that low temperatures can slow refueling by migrating birds is by diverting a greater proportion of energy accrued during foraging to thermoregulation (Wikelski et al. 2003). Torpor allows bats to somewhat decouple their daily energy

budgets from T_a , freeing them from some of the costs faced by birds (McGuire et al. 2014). However, *L. noctivagans* are pregnant during their spring migration (Druecker 1972), and female bats commonly use torpor to a lesser extent during pregnancy (Solick and Barclay 2006; Turbill and Geiser 2006; Stawski 2010; Dzal and Brigham 2012) but see (Chruszcz and Barclay 2002; Rintoul and Brigham 2014). Pregnant hoary bats (*Lasiurus cinereus*) captured during their spring migration defend a high body temperature over a wide range of experimental T_a (Cryan and Wolf 2003). If female *L. noctivagans* avoid torpor during spring migration, they would also incur a refueling penalty when they encounter low T_a .

The passage date of male bats did not appear to be constrained by cooler weather since there was no difference in mean capture date of males between the warmest and coldest years. This pattern would be expected if males have the low, predictable daytime energy costs associated with using torpor, and rely predominantly on pre-migration energy stores as fuel. A similar strategy is seen in both sexes during autumn migration (McGuire et al. 2014). Future work should experimentally test sex differences in the thermoregulatory responses of spring migrating *L. noctivagans*.

Three potential mechanisms may underlie the observed sex difference in migration timing I observed. First, there could be latitudinal segregation of sexes on wintering grounds. However, there is no compelling evidence of geographic sex segregation in wintering *L. noctivagans* (Cryan 2003; Perry et al. 2010). I cannot rule out the possibility of latitudinal sex segregation during the wintering period because the occurrence data are far from complete and the winter habitats of the population migrating through Long Point are unknown. Second, females could depart from wintering grounds earlier than males. Museum collections suggest that female tree-bats do initiate their northward migration before males (Cryan 2003). Third, females could migrate more quickly than males. It seems unlikely that females migrate more rapidly than males because my data suggest that females are affected more than males by cold weather through an indirect effect on refueling (see previous section). If females require more frequent or longer refueling periods than males, this would result in an overall slower pace of migration. If the

observed difference in migration timing at Long Point is a product of earlier departure, but a slower migration pace by females, I predict there will be a greater difference in male and female passage dates through sites at locations closer to the beginning of their migration, a subject for further research.

2.5.1 Body composition

Bats carried smaller fat stores in the spring (11% of body mass; this study) than they did at the same site during autumn migration (19% of body mass; McGuire et al. 2011). The relatively larger autumn fat stores would be expected if *L. noctivagans* also require these fat stores after migration, to sustain hibernation. Alternatively, this seasonal difference in body composition could relate to how close bats are to the end of their migration. Bats caught in the autumn are expected to travel to the southern United States (Perry et al. 2010) or eastward to more moderate coastal climates, similar to overwintering populations of *L. noctivagans* in British Columbia (Nagorsen et al. 1993). In contrast, spring migrants may potentially have almost reached the end of their journey when captured at Long Point if their summering grounds are in southern Ontario (Parsons et al. 1986), and may thus have depleted more of their fat stores.

Fat stores of female bats were nearly double the mass of those of males in two of the study years. This result is striking because previous studies at the same site have reported no sex difference in *L. noctivagans* fat stores during autumn migration (McGuire et al. 2011; 2014). Two hypotheses (insurance versus reproductive) could explain the greater fat stores of female bats.

Sandberg and Moore's (1996) insurance hypothesis, posits that fat is needed to weather harsh environmental conditions early in the season, and makes several predictions relevant to my study. First, if there is no sex difference in phenology, there will also be no sex difference in fat stores. I found no sex difference in passage date of bats in 2013, but females still had larger fat stores than males in this year. Second, earlier migrants will have larger fat stores to withstand harsher conditions. I observed no correlation between capture date and fat stores in either sex in any year. Early arrivers were not those with

greater energy stores. Third, greater fat stores will be evident in colder years. In my study, female bats carried the largest fat stores in years when the average T_a was the mildest, and there was no directional relationship between T_a and male fat stores. Overall, I find little support for the predictions of the insurance hypothesis for *L. noctivagans*. Bats are well-known for their extensive use of torpor, and this may provide sufficient insurance against inclement weather. Though bats frequently avoid torpor while pregnant, they remain capable of using it during emergencies (i.e., unseasonably low T_a). Pregnant female hoary bats have been observed dropping into deep, multiday torpor during spring storms (Willis et al. 2006).

The reproductive hypothesis predicts that females will have greater fat stores than males, and that there will be no correlation between arrival date and fat mass. In two of the three study years, females had significantly larger fat stores than males, and in one year there was no sex difference. This is consistent with the reproductive hypothesis, as I also found no correlation between arrival date and fat. I hypothesize that females defend a minimum fat threshold that exceeds that of males, and that females delay migration to keep fat stores above that threshold. While temperature predictably delayed the arrival of female bats, it did not have a comparable linear effect on their fat stores. In 2014, the coldest year, female fat stores were comparable to 2013, but mean female arrival date was seven days later.

The size of fat stores remaining after migration may have substantial impacts on the reproductive success of female bats. Female *Myotis lucifugus* maintain larger fat stores than males in late hibernation, presumably because there is a benefit of conserving fat for use during reproduction (Jonasson and Willis 2011). Remaining fat stores may allow *L. noctivagans* to maintain T_b that would speed fetal development. Larger fat stores are proposed to allow American redstarts (*Setophaga ruticilla*) to invest time in other activities such as territory defense, or focus foraging efforts on accruing essential micronutrients (Smith and Moore 2003). Similarly, bats with greater fat stores are able to invest more time in searching for suitable maternity roosts (instead of foraging) when they first arrive on the breeding grounds. Roost searching is particularly important for

tree-bats because cavities in decaying trees are less predictable from year to year than are buildings or cave roosts. Females may begin migration with larger fat stores retained over winter, similar to the ‘thrifty female’ strategy seen in *M. lucifugus* (Jonasson and Willis 2011), or accumulate this fat *en route* by increasing foraging.

The fat stores of females were more variable than those of males in my study. This pattern could be caused by sex differences in refueling strategies. If males carry small fat stores, replenish them with brief nightly foraging bouts, and have predictable, low daytime energy costs (through torpor use), then they would be expected to maintain relatively constant fat stores. If female *L. noctivagans* use torpor to a lesser extent, their thermoregulatory costs will depend on T_a (like all homeotherms) and their thermoregulatory costs will be greater, but also less predictable. Females would be expected to have a wider distribution of fat stores if they are captured at various stages of refueling.

In summary, sex differences exist in the time and energy investments made by migrating bats in spring. Females carried the largest fat stores in years when they arrived earliest. Cold temperatures delayed the migration of females, and likely resulted in an energy penalty. The opposite trend was seen in males, where the relatively earlier arrival of males in 2012 coincided with smaller fat stores. Males appear to “pay” for earlier arrival (as compared to male arrival date in other years) by depleting fat stores, which suggests that males are more reliant on energy acquired prior to migration. I propose that females partially fuel spring migration with *en route* foraging, while males are able to migrate using resources leftover from overwintering. Predicting the potential effects of climate change and habitat degradation on these species requires knowing which habitats they rely upon throughout their annual cycle. Differences in phenology observed among the three years of my study emphasize the importance of collecting ecological data over multiple years, and open up interesting questions about how bats respond to changes in their environment. Future studies are required to explore how environmental factors mediate changes in the migration timing of bats and the extent to which these carry-over effects impact population recruitment.

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CHAPTER 3

EVIDENCE FOR SPRING STOPOVER REFUELING IN MIGRATING SILVER-HAIRED BATS (*LASIONYCTERIS* *NOCTIVAGANS*)

3.1 ABSTRACT

The fuel strategies used by migrating bats are not well understood, as there is limited evidence regarding whether they forage on the wing while migrating (fly-and-forage migration), avoid refueling at stopovers by minimizing roosting energy costs (torpor-assisted migration), or actively refuel during multi-day stopovers. Further, these migration strategies of bats have been explored previously in the autumn, but not during the spring when insectivorous bats face low food abundance. I captured migrating *Lasionycteris noctivagans* at a stopover site in Long Point, Ontario, Canada in April and May of 2012-2014. I followed the movements of 40 bats (male N=18; female N=22) outfitted with radio transmitters using an automated telemetry array. I examined the effects of fat stores, sex, and ambient temperature (T_a) on stopover duration. As seen previously in autumn, most bats departed the evening following capture, but one third of bats were non-transient and used multiday stopovers. Extended stopover was associated with lower T_a . There was no effect of sex or fat on stopover departure probability. I used nightly mass gain of bats captured a single time to examine refueling. Bats captured closer to dawn had greater fat and lean masses than those captured early in the night, a trend indicative of mass gain at this site. Mine is the first study to provide evidence that bats use stopover habitat for refueling.

Key words: automated radio-telemetry, Chiroptera, migration, migratory strategies, refueling, torpor

3.2 INTRODUCTION

Migrating animals must partition time and energy between fuel acquisition and migratory movement, but how this is achieved can vary greatly. Optimal migration theory, originally developed for birds, posits that avian migrants balance the currencies of time and energy mainly by adjusting flight speed, fuel load, and stopover duration (Alerstam and Lindström 1990; Hedenström and Alerstam 1997; Hedenström 2009; Alerstam 2011). Bats, as flying endotherms may behave similarly to birds, but the potential to fuel while flying (Šuba et al. 2012), or use torpor to minimize energy loss during stopover (McGuire et al. 2014) may lead to different behaviours and physiology than predicted.

Fuel management decisions of migrants can depend on the distribution of resources across the landscape and the foraging ecology of a species. At one extreme, the Bar-tailed Godwit (*Limosa lapponica*) internally deposits its entire fuel load (40% of body mass is fat) and makes a single ~ 11,000 km transoceanic flight from New Zealand to Alaska (Gill *et al.* 2009). Short-hop migrants, including many songbirds, have access to many foraging sites and intersperse movement with periods of intense foraging at stopovers before the next leg of the journey (Newton 2008; Sawyer and Kauffman 2011). Ungulates are able to forage while migrating, but use stopover periods to take advantage of patches of good refueling habitats along their migration route (Sawyer and Kauffman 2011). Fly-and-forage migrants are able to combine foraging flight and migratory flight, i.e., species that hunt on the wing – aerial insectivores, some raptors and many seabirds (Strandberg and Alerstam 2007; Strandberg et al. 2009; Dias et al. 2012). Some aerial insectivores (e.g. Common Swifts, *Apus apus*) adopt a mixed strategy, combining fly-and-forage with periods of stopover (Åkesson *et al.* 2012), while other aerial insectivores (e.g. barn swallows, *Hirundo rustica*) have thus far only been documented using a stopover strategy (Gill *et al.* 2005).

The migration strategies of insectivorous bats remain poorly understood. Many bats may not need to make discreet stopovers because, as aerial insectivores, they can hunt while migrating. McGuire et al. (2011) proposed that the silver-haired bats (*Lasionycteris noctivagans*) make brief stopovers of < 24 h, refueling for only a few minutes at dusk

before initiating a migratory flight. These authors hypothesized that bats had sufficient fat stores to theoretically complete migration without refueling because torpor lowered their daytime energy costs (McGuire et al. 2011; 2014). This hypothesis could prove to be wrong because the degree to which the fat stores, measured by McGuire *et al.* (2011), are available to fuel migration is difficult to ascertain; a proportion of fat stores amassed on the summering grounds may be required to sustain hibernation. Nathusius's pipistrelle (*Pipistrellus nathusii*) appears to use a fly-and-forage migration strategy, frequently interrupting migratory flight to forage along the coast of the Baltic sea (Šuba *et al.* 2012). Studies of stable isotopes in the breath support this fly-and-forage hypothesis. *P. nathusii* employ a mixed fuel strategy – fueling flight with recently digested food in the early evening and transitioning to fat stores near dawn (Voigt *et al.* 2012). If *P. nathusii* used stopovers, then isotope analysis would be expected to reveal that bats rely only on fat stores to fuel flight (unless bats were sampled at a stopover site). The above studies on bats were conducted during autumn migration, when insects are relatively abundant as compared to spring migration. Because the ease of energy acquisition is a key factor for determining how animals allocate time, where they stop, and for how long, seasonal differences in prey abundance are expected to affect migration strategy. For example, red-backed shrikes (*Lanius collurio*) use different migration routes in autumn as compared to spring to take advantage of favorable foraging conditions on the northern savannah, stage for longer periods of time, but move more rapidly (Tottrup *et al.* 2012).

The aim of this study was to investigate the use of stopover sites by *L. noctivagans* during spring. I returned to the same stopover site, in southern Ontario, Canada, where previous work was conducted on the species in the autumn (McGuire et al. 2011; 2014). I hypothesized that the inferred difference in food availability in spring, caused by lower temperatures, would affect the way bats refuel.

My first objective was to determine if ambient temperature (T_a), fat stores, and sex affect stopover duration in spring. One of the few studies of spring migrating bats found that most *L. noctivagans* occupied roosts for a single day unless the weather was very cold, or it was raining (Barclay et al. 1988). However, the methods used in that study were not

suitable to measure stopover duration, as any roost switching would be mistaken for a departure. I predicted that cold weather would result in extended, multi-day stopover periods in spring migrants. Cool spring T_a decreases flying insect abundance and will in turn diminish foraging opportunities (Taylor 1963; Holyoak et al. 1997; Benton et al. 2002), possibly to such an extent that fly-and-forage migration is no longer profitable. Migrants are theorized to depart stopovers once they have acquired sufficient fuel stores (Alerstam and Lindström 1990). So, I further predicted that within the spring migration season, colder T_a will extend stopover because low refueling rates extend stopover durations (Alerstam and Lindström 1990). Additionally, I predicted fat stores to be negatively correlated with stopover duration as bats with small fat stores would require more time to rebuild them. Finally, I predicted that females would have briefer stopovers than males. Female bats arrive earlier in the migration season than males (Chapter 2), likely because there is an advantage to arriving on the summering grounds early to raise their pups (Frick et al. 2010). Female bats may achieve this earlier arrival by speeding refueling and in turn likely shortening the duration of their stopovers, a similar strategy is used by some male birds rushing to secure breeding territories in the spring (Seewagen et al. 2013). In summary, I predicted: 1) spring migrants would make longer stopovers than in autumn, 2) cold T_a would extend stopover duration, 3) bats with small fat stores upon arrival would have longer stopovers, and 4) females would have shorter stopovers than males.

My second objective was to determine if bats refuel at stopover. Several studies have examined mass changes of birds recaptured on migration (e.g., Mueller and Berger 1966; Moore and Kerlinger 1987; Loria and Moore 1990; Kuenzi et al. 1991), but these studies require a massive mark recapture effort that is not feasible for migrating bats. Further, birds that are recaptured may not be representative of the population; they often have smaller fuel stores than birds captured once and so may be of poorer quality (Moore and Kerlinger 1987; Loria and Moore 1990; Kuenzi et al. 1991; Bonter et al. 2007). An alternative method is to regress mass on first capture against the time of day, if migrants at a site are gaining mass, then the slope should be positive. Increases in mass of the population over the day are assumed to represent the daily gain of all individuals (e.g.,

(King 1976; Winker et al. 1992; Dunn 2000; Bonter et al. 2007). I use this second approach to examine the nightly mass gain of bats using a 3-year dataset. If bats are depositing fat stores at my site, I predicted that bats captured later in the night would be heavier than those captured early in the evening.

3.3 METHODS

L. noctivagans (LeConte, 1831), the silver-haired bat, is a small insectivorous tree-roosting bat (Kunz 1982). Evidence for migration in *L. noctivagans* comes primarily from seasonal shifts in distribution (Cryan 2003) and stable isotopes (Baerwald et al. 2014), however the connectivity between summer and winter populations remains unknown. The Long Point Bird Observatory, ON, Canada (42°34'N, 80°20'W) has been established as a reliable point for capture of autumn migrating *L. noctivagans* (Dzal et al. 2009). My study site is on average 10.8 °C cooler during the spring migratory period (April and May: 10.4 °C) than in the fall (mid-August to mid-September: 21.1 °C; Long Point Environment Canada weather station five year average, 2008-2012). For more information about the capture site, see Chapter 2. I used monofilament mist nets to catch bats during the spring migration period: April 3-May 31, 2012; April 14-May 27, 2013; and April 4-June 5, 2014. Nets were opened nightly throughout the study season from dusk until dawn unless there was rain, high winds, or T_a below 3 °C (I captured no bats below 5 °C in the first year of the study).

For each bat, I used quantitative magnetic resonance (QMR) body composition analyzer (EchoMRI-B; Echo Medical Systems, Houston, TX, USA) to non-invasively measure dry fat mass and wet lean mass (McGuire and Guglielmo 2010). QMR measurements are taken by placing an unrestrained bat in a small ventilated tube, which is then inserted in the bore of the QMR machine for three replicates of a 2-minute scan (for details see McGuire and Guglielmo 2010). Previous work has shown no impact of the QMR on the navigational abilities of bats (McGuire et al. 2011). After the QMR scan, I affixed radio-transmitters to a fur trimmed region on the bats' upper back using a non-toxic latex glue (Ostobond; Ostomy Quebec), which wears off in approximately 30 days. The transmitters weighed 0.29 g and bat masses ranged from 8.9 – 14.6 g, so transmitter

weights ranged from 2.0 – 3.6 % of the body mass of the bats, which is less than the accepted guideline of 5 %, to prevent loss of maneuverability that would impede foraging (Aldridge and Brigham 1988). I used coded radio transmitters (NTQB-1 Lotek, Newmarket, ON), which enabled us to continuously monitor the location of all study individuals. The coded transmitters broadcast on a single radio frequency and emitted a pulse signature unique to each transmitter at 12 second intervals.

3.3.1 Stopover duration

To establish when bats departed the stopover region, I used an array of five (2012) or eight (2014) automated radio-receiving stations (Fig. 3.1). Each station was comprised of a telemetry receiver equipped with 1-3 directional antennas (9-element, Yagi), mounted on a 9 m tower. Directional antennas have the strongest radio wave detection beam in the forwards direction, a lesser detection beam in the backward direction, and much lower detection laterally. Lotek receivers (SRX 600, Lotek Engineering Inc., Newmarket, Ontario) were used in 2012 and SensorGnome receivers (www.sensorgnome.org) were used in 2014. The estimated detection range of each antenna was 14 km (based on concurrent detections of a bat by two towers using the same equipment as McGuire et al. (2011)). Bats were considered to have completed their stopover when they left the detection range of the tower at the capture site (Oldcut) and were not subsequently re-detected within the local array. Bats that departed within 24h were classified as ‘transient’ and those that stayed longer as ‘non-transient’.

3.3.2 Stopover behaviour

The automated radio telemetry system occasionally allowed us to detect detailed activity patterns from individuals that roosted in the proximity of the Old Cut telemetry tower (N=9). For these individuals I was able to determine if they left their roost on a given night by examining the variability in signal strength. The transmitters of roosting bats broadcast a constant, low signal strength, because roosts were often low to the ground or sheltered within buildings. Variable signal strengths are indicative of non-directed flight and are likely associated with foraging behaviour (Supplementary Fig. 3.1).

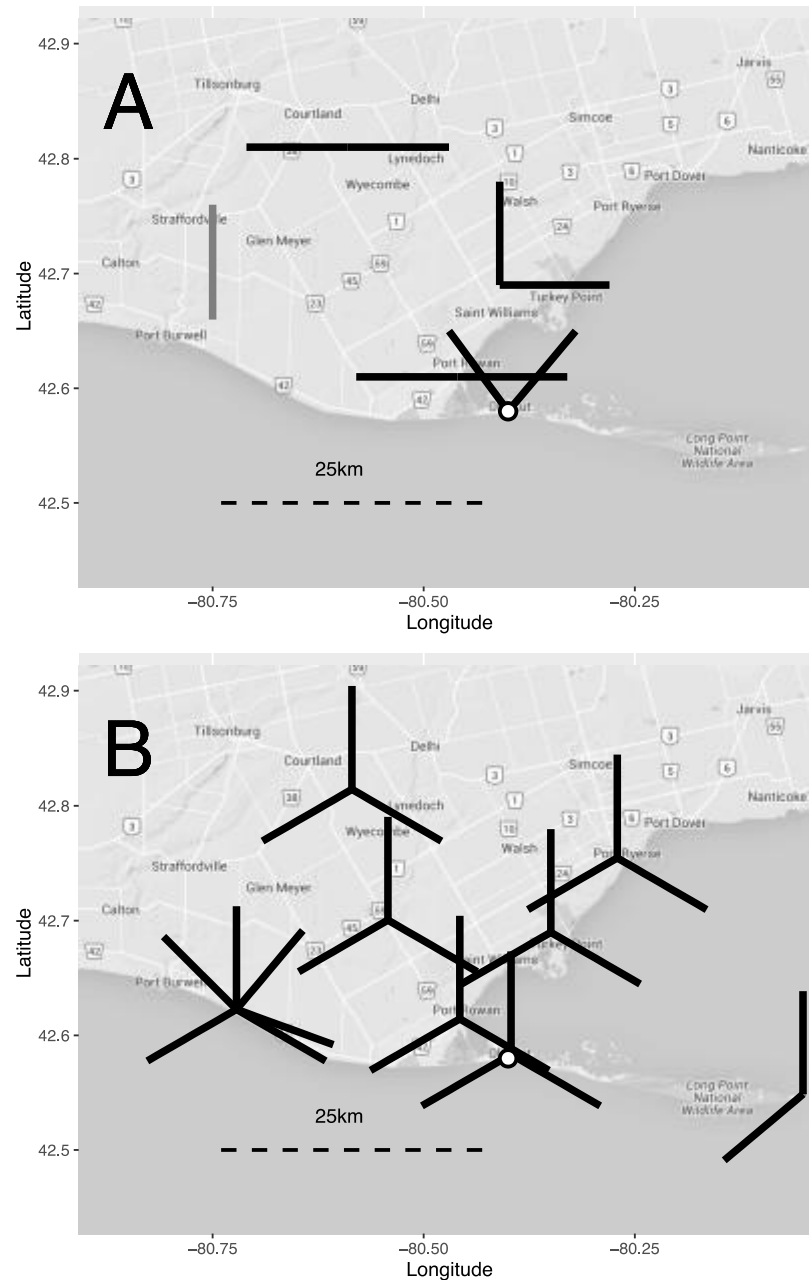


FIG. 3.1– Map of the study region Long Point, Ontario, Canada in A) 2012 and B) 2014. Bats were captured at the bird observatory (circle) and tracked until they left the stopover site, which is delineated by the perimeter of receiving stations. Positioning and estimated detection range of antennae on receiving stations are shown by black bars. The grey bar denotes the one receiving station, which was not functioning during the study.

Absent bats may have left the detection range of the tower, or may have been roosting in a very sheltered space. In 2012, I searched for bats during the day to confirm their presence in roosts, if a bat was not detectable by the Old Cut tower, but was roosting nearby then I can reason that it did not leave its roost the previous evening as its departure flight would have been detected.

All research activities were approved by University of Western Ontario Animal Care Committee (protocol 2010-020; Appendix D), and were permitted by a Wildlife Scientific Collector's Authorization from the Ontario Ministry of Natural Resources (authorization no. 1067554, 1073065 and 1076439; Appendix E).

3.3.3 Analysis

I modeled stopover using a survival analysis framework, analyzing the “risk” that a bat would depart the study site using Cox Proportional Hazards (CPH) models, which are semi-parametric survival models. Higher risk is interpreted as a higher chance of a higher probability of departure and so shorter stopover durations. The full model included sex, fat mass (g), year, and night-time mean temperature experienced during stopover. The importance of model covariates was assessed with 95% confidence intervals.

Hourly temperature data (± 0.1 °C) were obtained from the Bird Studies Canada weather station (42°36'50''N, 80°27'29''W) 6 km from my capture site, and within the perimeter of stopover stations (Fig. 3.1). CPH models were also used to examine the relationship between fat stores and length of stay in two subsets of bats that arrived at the stopover site on the same day. One-way ANOVA was used to compare the nighttime T_a on nights when bats were active, departed or roosted in close proximity to the Old Cut tower.

I regressed the time of night bats were captured against fat and lean mass to estimate rates of nightly mass gain. Statistical analyses were conducted in the program R (version 3.2; R Development Core Team 2009). I used the *coxph* function of the package *survival* for CPH. All values are reported as mean \pm standard deviation, N = number of individuals.

3.4 RESULTS

3.4.1 Stopover duration

Radio transmitters were deployed on 40 *L. noctivagans*, 24 bats in 2012 (N=13 male; N=11 female) and 16 bats in 2014 (N=5 male; N=11 female). I quantified stopover duration for 35 bats (N=15 male; N= 20 female). In 2012 three male bats remained in the study region for more than 35 days (approx. transmitter battery life). This observation was not attributable to death or transmitter loss because bats were recaptured and continued to move within the study site. These individuals were classified as residents, and excluded from subsequent analyses. In 2014 data were missing from two bats tagged on April 15th when there were technical difficulties with the Old Cut receiver.

Stopover duration of bats ranged between 1 and 21 days (3.6 ± 5.3 days, median 0.8 days; Fig. 3.2). The majority of bats were transients, 64% of captures, departed the same evening they were captured, or the following evening if captured near dawn (i.e. stopovers were < 24 h). Multi-day stopovers could not be entirely attributed to inclement weather (e.g., rain or high winds), as there were several nights when some bats departed and others remained (Fig. 3.3). Each increase in 1 °C of night-time mean temperature was associated with a 1.2 times greater daily departure probability (hazard ratio [HR_{Temp}] = 1.2, 95% CI 1.1, 1.3; Fig. 3.4). I found no difference in the daily probability of departure between male and female bats (HR_{Sex} = 0.6, 95% CI = 0.1, 2.6), between years (HR_{Year} = 0.9, 95% CI = 0.5, 1.5), or by fat mass (HR_{Fat} = 0.9, 95% CI = 0.3, 2.3).

In both 2012 and 2014 there was a group of 4-6 bats that arrived on the same night (Fig. 3.3). I used these individuals to further explore the effects of fat stores on stopover duration, when all individuals experienced the same weather conditions. Within these cohorts there was no increase in the daily probability of departure by fat mass in either 2012 (HR_{2012fat} = 1.4, 95% CI = 0.1, 23.7) or 2014 (HR_{2014fat} = 0.2, 95% CI = 0.2, 242.2).

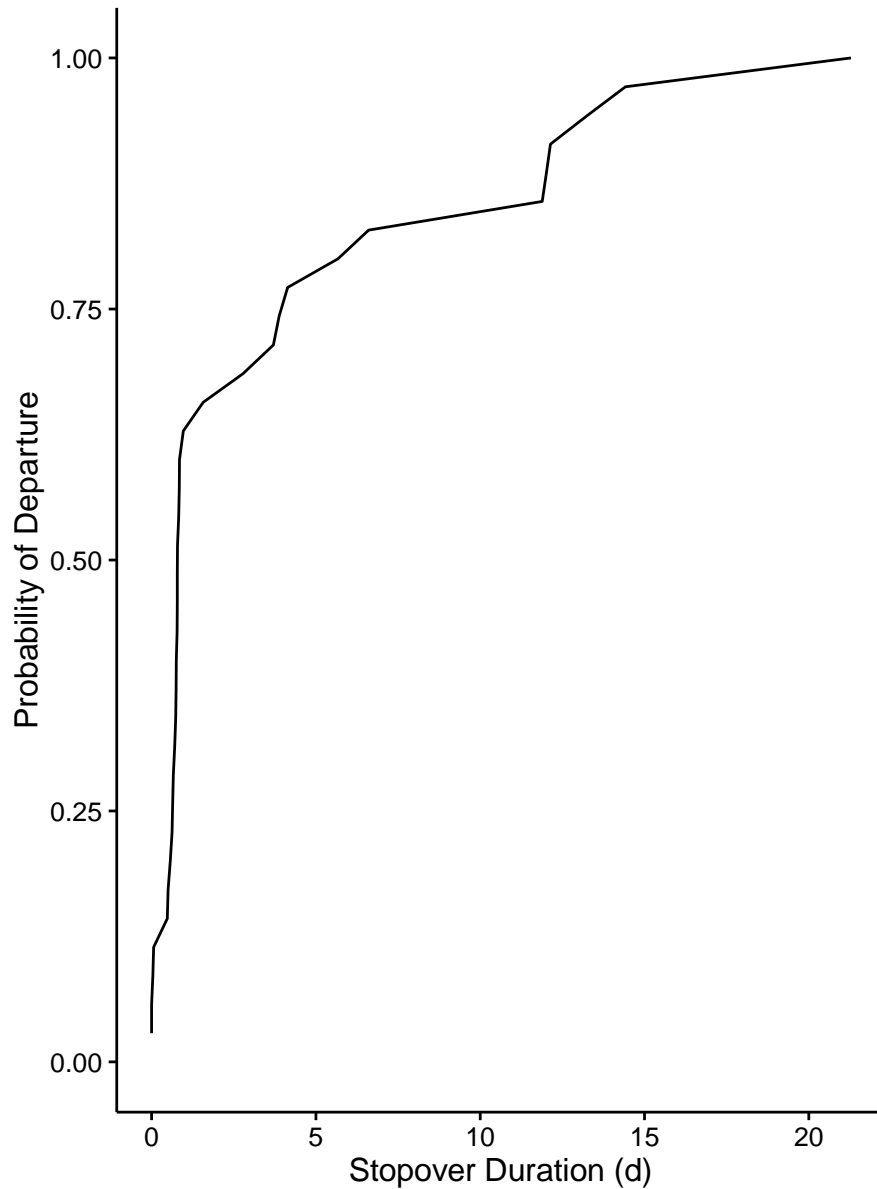


FIG 3.2– Probability of departure of *L. noctivagans* from a stopover site during spring migration (April – May, 2012 – 2014). Grey shading denotes 95% confidence interval. A single day stopover indicates a bat that remained at the site for a single day (inactive period), less than one stopover day indicates the bat departed on the same night of capture.

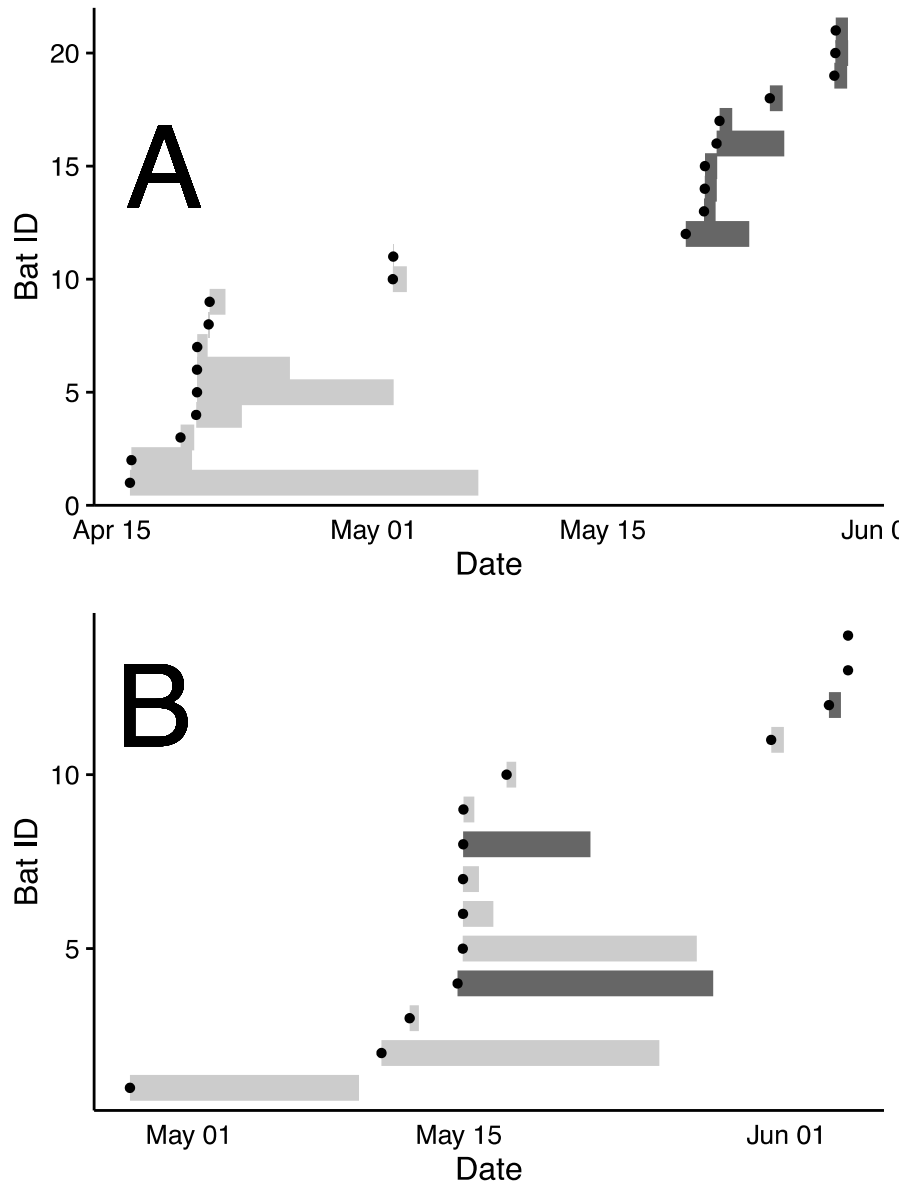


FIG 3.3– Time periods that *L. noctivagans* arrived and departed the stopover site in A) 2012 and B) 2014. Bats arrived in pulses of individuals, but remained at the stopover for different lengths of time. Points show when bats were captured and solid lines are the time period when bats were detectable within the region. Males are shown in dark grey, females in light grey. Note the different x-axis time scales.

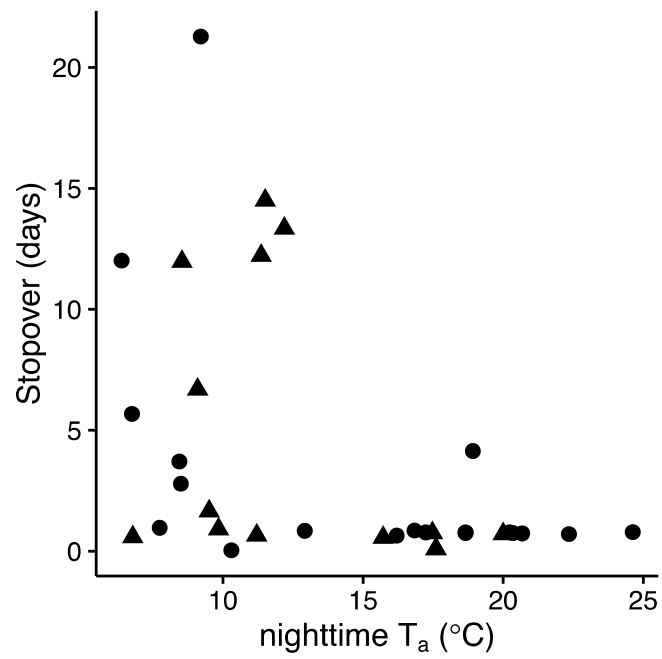


FIG 3.4— Relationship between *L. noctivagans* stopover duration and average night-time T_a experienced during stopovers. Multiday stopovers are more common when bats experienced T_a below 15 °C. Circles mark 2012 and triangles mark 2014.

3.4.2 Stopover behaviour

Bats that had multi-day stopovers spent several of those nights inactive and presumably roosting (Table 3.1). T_a differed on nights when bats were roosting, active or departed the study site ($F_{2,82} = 5.4$, $P < 0.01$). Nights on which bats were active were 3 °C warmer than nights when they roosted ($P = 0.01$). Nights when bats departed did not differ significantly from those on which bats were active ($P = 0.9$) or when they roosted ($P = 0.1$).

3.4.3 Nightly mass gain

Over three years I captured a total of 114 bats (66% female, 34% male). Bats were captured throughout the night, with a small peak shortly after dusk and a larger peak about 1 h before dawn (Fig. 3.5). Bats carried on average $11.3 \pm 4.6\%$ body fat. Time of night at which bats were QMR scanned had a significant effect on both fat and lean mass, which suggests that bats were gaining mass throughout the night. Fat mass was positively correlated with time of night, fatter bats were captured closer to dawn ($P = 0.006$, $F_{1,82}=7.9$, $R^2=0.09$; Fig. 3.6a). Lean mass was also greater in bats captured later in the night ($P = 0.001$, $F_{1,82}=10.9$, $R^2=0.12$; Fig. 3.6b). There was no effect of sex on the slope of fat or lean mass, males and females gained mass at equal rates ($P > 0.05$).

For each hour later in the night that a bat was captured, its fat and lean mass were 0.098 g and 0.090 g greater, respectively. If bats put on mass at this rate, then in the eight hours between sunset and sunrise, bats would be expected to put on 1.50 g of mass or approximately 10-17 % of their body weight. Forearm length did not vary with hour of capture, indicating that hourly mass change was not driven by larger bats being captured later in the night ($P = 0.54$). The relative deposition of fat (0.44 /g body mass) and lean mass (0.49 /g body mass) did not differ between the sexes ($P > 0.05$; Fig. 3.7).

Table 3.1– Nighttime activity patterns of bats during multi-day stopovers. Missing bats are presumed to be in an unknown roost, or outside of the range of the tower.

	Tag id	Sex	Fat mass (g)	Roosting (nights)	Active (nights)	Missing (nights)
2012						
	89	Female	1.88	7	12	1
	146	Female	2.52	4	0	0
	87	Female	1.08	8	4	0
	144	Female	2.27	4	1	0
	94	Male	-	0	4	1
2014						
	377	Male	0.78	11	2	0
	406	Female	1.24	0	4	7
	408	Male	0.77	5.5	0.5	0
	411	Female	2.02	7	4	0

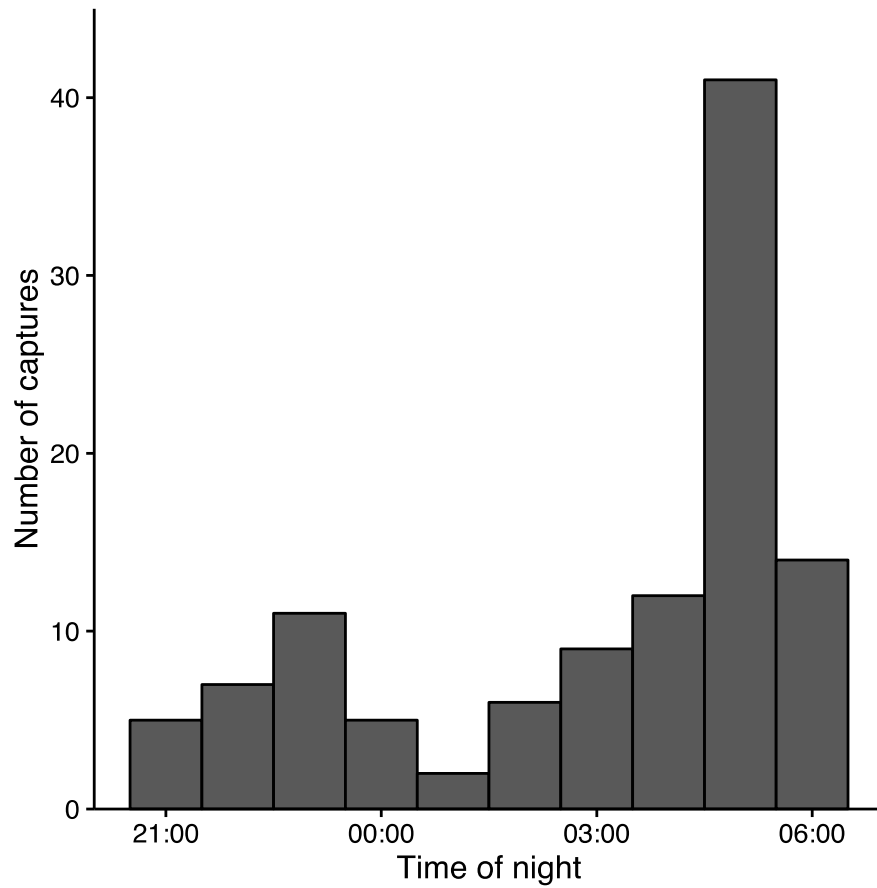


FIG. 3.5— Time of night *L. noctivagans* were captured at Long Point (2012 – 2014) form two peaks, one shortly after sunset and the greatest number of captures occurred in the hour before dawn. Netting effort was constant throughout the night.

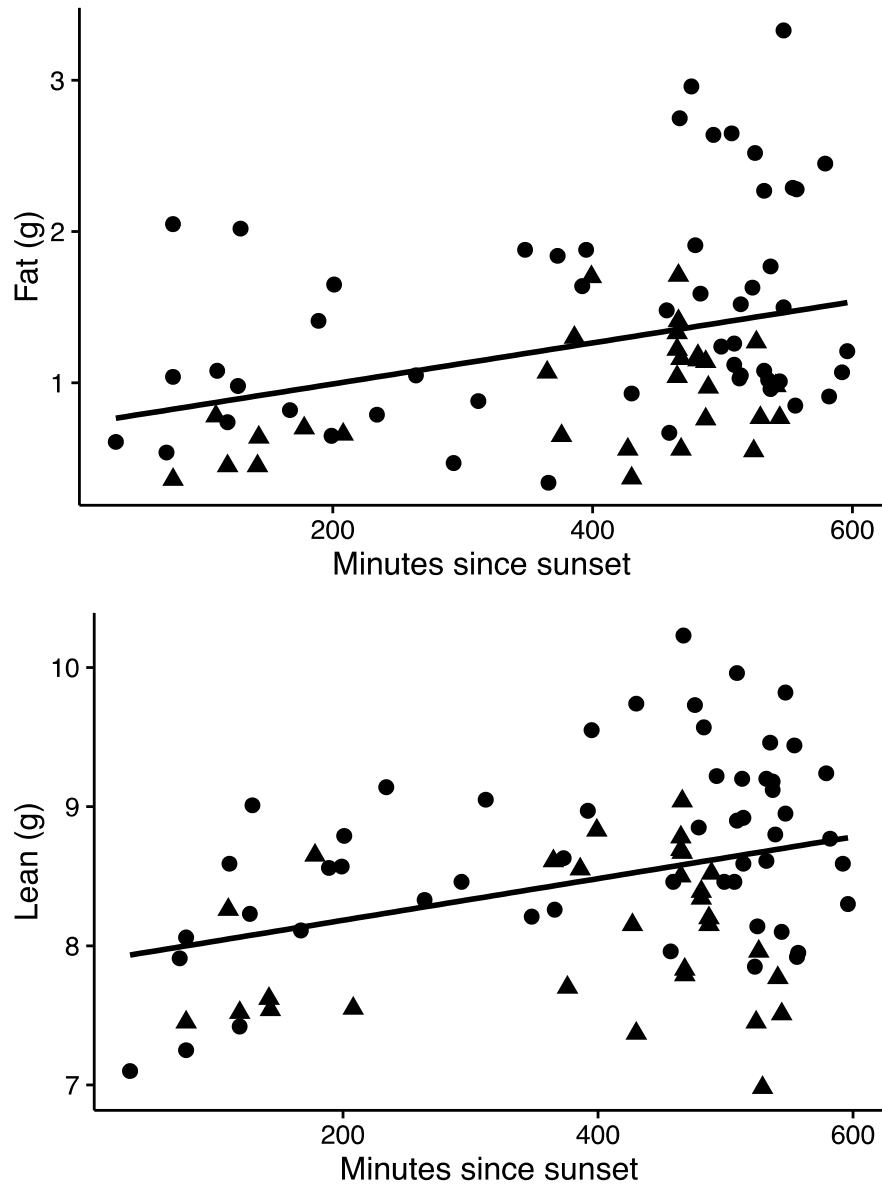


FIG. 3.6— Quantitative magnetic resonance measurements of fat ($R^2 = 0.11$; $P = 0.006$; $y = 0.00136x + 0.721$) and lean ($R^2 = 0.12$; $P = 0.001$; $y = 0.00150x + 7.884$) mass regressed against time capture for female (circles) and male (triangles) *L. noctivagans* during their spring migration. There was no effect of sex on rate of mass gain ($P > 0.05$).

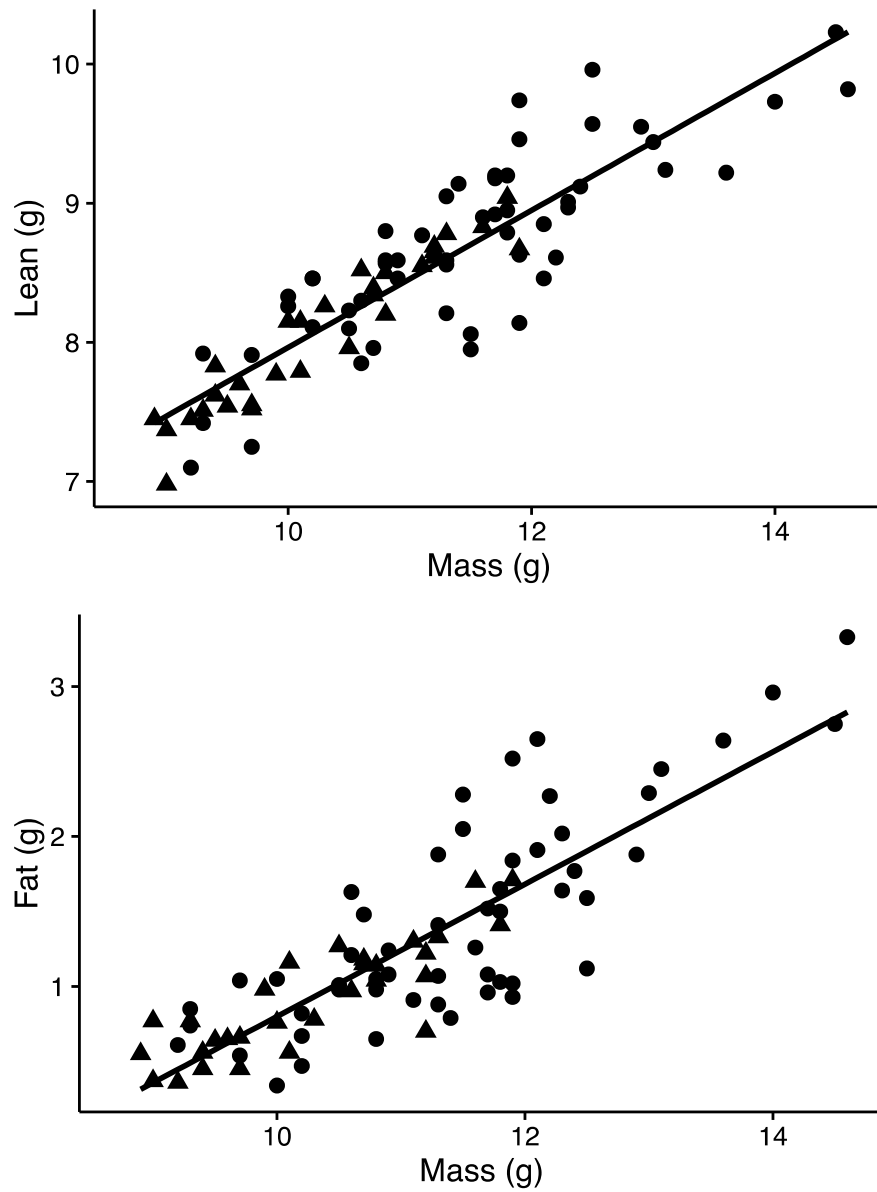


FIG. 3.7– Deposition of lean ($R^2=0.71$; $0.48x + 3.12$) and fat ($R^2= 0.79$; $y =0.45x- 3.62$) masses of female (circles) and male (triangles) *L. noctivagans* during spring migration. There was no effect of sex on mass deposition.

3.5 DISCUSSION

Bats used extended stopover periods during spring migration. Many bats were transient and departed the capture site in less than 24 hours, as found previously in autumn. However, about one third of *L. noctivagans* remained at the study site for more than one day. I hypothesize that *L. noctivagans* has a mixed migration strategy – using multiday stopovers during cool weather and fly-and-forage migration when prey availability permits. Multiday stopovers were a combination of nights dedicated to foraging and nighttime roosting, perhaps entering torpor to “pause” migration when weather and prey abundance was unfavorable. Mixed migration strategies, when used by swifts, involve the inclusion of stopover to take advantage of a particularly abundant prey source (Åkesson *et al.* 2012). Bats appear to use stopover for the opposite reason – to focus efforts on foraging when prey abundance is low and the fly-and-forage strategy may not be advantageous. It is also possible that use of multiday stopovers in response to cool weather helps bats time their migration so that they do not arrive at breeding areas when conditions are still poor.

The proportion of transients (bats that did not stopover for multiple days; 64%) is comparable to that observed in migrating birds which use a stopover migration strategy e.g., white-crowned sparrows (*Zonotrichia leucophrys leucophrys*: 46%; Cherry 1982), European robins (*Erithacus rubecula*: ~50%; Bulyuk and Tsvey 2013), and wood sandpiper (*Tringa glareola*: 73.5%; Muraoka *et al.* 2008). The stopover durations used by *L. noctivagans* (3.7 ± 5.4 days) were also similar to those used by spring migrating passerine birds e.g., Swainson’s thrushes (*Catharus ustulatus*) – 3.7 ± 3.4 days (Matthews and Rodewald 2010), European robin (*Erithacus rubecula*) – 3.8 ± 4.8 days (Bulyuk and Tsvey 2013), and red-eyed vireo (*Vireo olivaceus*) – 2.80 ± 0.14 days (Cohen *et al.* 2014). Combined, these similarities in the proportion of transients and stopover duration suggest that during spring migration *L. noctivagans* use stopovers in a similar way to birds, and may not use a fly-and-forage strategy.

I detected no effect of sex on the proportion of transients or stopover duration. This result is at odds with the different phenology of male and female *L. noctivagans*, females arrive

earlier than males in the migration season (Chapter 2). In birds, protandry (earlier arrival of males) is sometimes achieved by shortening stopovers (Dierschke et al. 2005), so I expected female bats would have shorter stopovers than males. This lack of sex difference may be due to the small sample size and large variation in the stopover lengths that I measured. Alternatively, under the current foraging conditions females may be unable to move more rapidly than males, and instead females may achieve earlier passage times by initiating their migration earlier, as has been suggested by occurrence data (Cryan 2003).

If refueling drives stopover length in bats, the size of fat stores should in part determine the length of stay (Alerstam 2011). That is, fatter bats will require less time to top up their fuel tank. My results did not support this hypothesis, I found that fat did not predict the length of a bat's stopover. The avian literature on the relationship between fuel load and stopover duration is mixed. Several studies have found that fat birds depart sooner, consistent with the idea that birds have completed refueling (e.g., Biebach et al. 1986; Morris 1996; Gannes 2002; Goymann et al. 2010; Seewagen and Guglielmo 2010). Other studies have found no effect of fat on the length of stay (Kuenzi et al. 1991; Salewski and Schaub 2007; Tsvey et al. 2007). Studies that find a link between fat stores and stopover duration are often conducted near an ecological barrier i.e., ocean or desert crossings where there is strong selection pressure to build a sufficient fuel store to cross inhospitable habitat where refueling is not possible (e.g. Biebach et al. 1986; Goymann *et al.* 2010). In contrast, European robins experience ample foraging opportunities along their migratory route and show no relationship between stopover duration and fat stores (Tsvey et al. 2007). *L. noctivagans* likely experience frequent or continuous foraging opportunities along their route, and so may not need to amass large fuel stores before departure. Other migrating bat species which cross ecological barriers such as the Baltic Sea (Rydell et al. 2014) may show a stronger relationship between stopover duration and fuel load. Although, some bat species have been reported to forage for insects up to 14 km from shore (Ahlén et al. 2009) and may be able to continue to use a fly-and-forage strategy over water.

Bats used multi-day stopovers during the cool, early spring season. Several passerines also tend to have longer stopovers during the early spring when there may be less time pressure to reach the breeding grounds (Dierschke and Delingat 2001; Matthews and Rodewald 2010). Prolonging stopover periods when faced with cold conditions may help bats and birds time their arrival to the development of resources at the summering grounds. During their migration *L. noctivagans* readily enter torpor, a state of decreased metabolism and body temperature that drastically reduces thermoregulatory costs (Chapter 4; McGuire et al. 2014). I observed several nights when bats did not leave their roosts and were likely torpid. The ability to use torpor could substantially mitigate the risks of arriving too early. Whereas most birds risk depletion of fat reserves and starvation if they arrive at stopover sites while refueling prospects are still poor, bats may be able to “pause” migration during unfavorable periods and wait until refueling opportunities improve. Birds that use torpor, such as nightjars and hummingbirds may also be able to “pause” migration similar to bats (Carpenter and Hixon 1988; Doucette et al. 2011). *L. noctivagans* remained at stopover for longer periods when T_a dropped below 12°C, and coincidentally, 10°C is approximately the onset for insect flight and likely indicative of poor foraging prospects (Taylor 1963). The extension of stopover and delay of migratory movements during cold weather could explain why female passage timing is later in cold years (Chapter 2). Males migrate later in the season, reducing the likelihood of encountering cold weather, and so their passage timing is independent of T_a (Chapter 2).

Use of multi-day stopovers during spring contrasts with the migration strategy of *L. noctivagans* at the same site during the autumn, when nearly all bats departed after a single day (McGuire et al. 2011). Environmental conditions were sufficient to explain this seasonal difference in stopover behaviour. Bats remained at stopover for longer periods when T_a dropped below 12°C, a condition that was not frequently met during the autumn migration sampling period of McGuire et al. (2011). Further study later in the autumn migratory period (i.e. October) may reveal that multiday stopovers are also used at this time. Bats may be able to refuel more rapidly during warm fall nights than in the spring when cooler temperatures limit aerial insect abundance. There is limited evidence

that fall migrants were active (and presumably foraging) at my study site for more than one hour a night (McGuire *et al.* 2011). Seasonal differences in stopover are unlikely related to the position of Lake Erie relative to the direction of flight. If the lake were acting as a barrier I would predict the opposite pattern, that bats would spend longer periods building up fat stores in preparation to cross the lake (i.e., during autumn migration).

I provide the first evidence that like some bird species, bats may also stop for prolonged refueling under the right conditions. My telemetry data show that some bats spend several nights at a time with activity patterns likely associated with foraging. If bats were putting on mass throughout the night, I predicted that time of capture would be positively correlated with mass. Both fat and lean mass were positively correlated with time of night, which indicates that bats rebuild both their fat and lean tissue as fuel. I detected no sex difference in rate of refueling. However, this may be due to the sensitivity of the analysis. Analysis of plasma metabolites, which show a finer time scale of foraging status have detected sex differences in refueling rates of birds (Seewagen *et al.* 2011), with males refueling faster.

L. noctivagans use multiday stopovers to refuel during spring migration, similar to many passerine songbirds. The use of stopovers is not mutually exclusive to torpor-assisted migration and/or fly-and-forage migration, which may also be important components of the migration strategies of bats. Conditions experienced at stopover habitats can have a strong influence on the speed of migration and ultimately the likelihood of survival of migrating birds (Russell *et al.* 1994; Hutto 2000; Newton 2006), similarly if bats are refueling as they migrate, they may also be constrained by the quality of stopover habitats they encounter along their migration.

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CHAPTER 4

COLD BREAKS: SEASONAL AND SEX DIFFERENCES IN DAILY TORPOR USE BY MIGRATING SILVER-HAIRED BATS (*LASIONYCTERIS NOCTIVAGANS*)

4.1 ABSTRACT

Torpor allows heterotherms to conserve energy that would otherwise be expended on thermoregulation. Facultative use of torpor appears to be an important element of how bats maintain energy balance while migrating. However, little is known about factors that affect torpor expression in migrants. I investigated the effects of season, sex and fat stores on the use of torpor by migrating silver-haired bats. Spring and autumn migrations present different challenges that are likely to modulate the expression of torpor. During spring, cool ambient temperatures (T_a) increase the costs of thermoregulation and decrease flying insect abundance, making refueling more challenging. Further, females are pregnant during their spring migration and may use torpor to a lesser extent to prevent reducing fetal development. First, I examined the torpor patterns of free-ranging spring migrating bats using temperature-sensitive radio-transmitters. Second, I conducted a respirometry trial of torpor use in spring migrants under a constant experimental temperature of 10 °C. Finally, I compared spring torpor expression by free-ranging bats with data previously reported for autumn migration. Torpor bout duration was negatively correlated with T_a . After accounting for the effect of T_a , spring migrants still had 14% longer torpor bouts than fall migrants. Females had 14% shorter torpor bouts than males in both seasons. I hypothesize that differences in foraging effort between males and females, and differences in prey abundance, predictability, and/or nutritional quality between spring and fall may drive the observed patterns of torpor expression.

Keywords: Chiroptera, heterothermy, energy balance, sex differences, thermoregulation, torpor-assisted migration, migration

4.2 INTRODUCTION

The high energy demands of euthermia become a liability when food resources are scarce. When heterotherms enter torpor the decrease in metabolic rate and corresponding reduction in body temperature allows them to subsist on relatively small energy stores, biding time until conditions improve. Daily torpor has long been considered a physiological response to adverse environmental conditions (e.g. food scarcity and/or harsh weather)(Wang 1989). Indeed, torpor can facilitate survival during natural disasters (Nowack et al. 2015), and the ability to endure such stochastic events has likely contributed to lower extinction rates in heterothermic species (Geiser and Turbill 2009; Hanna and Cardillo 2014).

Recently, the facultative functions of torpor have become more widely recognized (Geiser and Brigham 2012). For example, late-born juvenile dormice experience low food availability while they attempt to acquire sufficient energy for growth and hibernation (Giroud et al. 2012). By using torpor, food restricted juvenile dormice “catch up” in growth to juveniles fed ad lib (Giroud et al. 2012). Similarly, mulgaras (marsupial carnivores) enter torpor during pregnancy to build up fat stores for the more expensive lactation period (Geiser and Masters 1994). The facultative use of torpor by a migrant was first observed in hummingbirds (Carpenter and Hixon 1988). By entering torpor for the entire night, one Rufous hummingbird (*Selasphorus rufus*) was estimated to have conserved 10% of its total fat stores. The authors concluded this observation constituted a facultative use of torpor rather than an emergency strategy because the bird was very fat and could have balanced its energy budget by using torpor for just part of the night (Carpenter and Hixon 1988). Subsequent research has suggested that hummingbirds modulate their use of overnight torpor to facilitate fat deposition during migration. While refueling, hummingbirds show biphasic mass gain – during the initial days, mass is accumulated slowly and then just prior to resumption of migration, mass is put on more rapidly (Carpenter et al. 1993). This rapid phase was facilitated by a decrease in overnight mass loss, which is hypothesized to be driven by an increase in use of overnight torpor (Carpenter and Hixon 1988; Hou and Welch 2016). Similarly, migrating Blackcaps (*Sylvia atricapilla*) that dropped their body temperature several degrees

overnight were able to increase their body mass more rapidly than those which defended normothermia (Wojciechowski and Pinshow 2009). The use of heterothermy appears related to refueling state. Blackcaps which used heterothermy also had lower body masses, and thus lower fuel stores, than those that defended normothermia (Wojciechowski and Pinshow 2009). Migrating silver-haired bats (*Lasionycteris noctivagans*) use torpor to reduce daytime thermoregulation costs (McGuire et al. 2014). Torpor assisted migration is hypothesized to shorten refueling times, and may preclude the need for bats to use multi-day refueling periods (McGuire et al. 2011; 2014). However, little is known about how the expression of torpor in migrants is affected by season or individual traits.

Here I investigate the effects of season, sex and fat stores on the use of torpor by migrating *L. noctivagans*. Spring and autumn migrations present different challenges that are likely to modulate the expression of torpor. During spring, migrants experience cooler ambient temperatures (T_a) which should increase the costs of thermoregulation. Lower T_a also means lower flying insect abundance (Taylor 1963), making refueling more challenging. Environmental conditions result in migrants being more energetically constrained in spring than in autumn, and may potentially slow the pace of spring migration. Consequently, I predict that migrants will spend a greater proportion of time in torpor during the spring as compared to the autumn.

Seasonal differences in reproductive investment by male and female bats are likewise expected to impact torpor expression. Females are likely in the early stages of pregnancy when they undertake spring migration (Druecker 1972). Reproduction and torpor are not mutually exclusive (McAllan and Geiser 2014), but pregnant females of many bat species typically use shorter torpor bouts and defend higher body temperatures than non-reproductive females and males (Cryan and Wolf 2003; Solick and Barclay 2006; Turbill and Geiser 2006; Stawski 2010; Dzal and Brigham 2012), probably to facilitate fetal development. So, I predict that females will use torpor to a lesser extent than males during spring migration, but there will be no sex difference in the expression of autumn

migrants.

My first objective was to describe the torpor patterns of free-ranging spring migrating bats and examine the effect of sex and fat stores. Second was to conduct a respirometry trial of torpor use in spring migrants under a constant experimental temperature of 10 °C to control for differences in T_a when males and females arrived at the study site (Chapter 2). Finally, I compared spring torpor expression with data previously reported for autumn migration in McGuire et al. (2014).

4.3 MATERIALS AND METHODS

This study was conducted at the Old Cut field station of the Long Point Bird Observatory, Ontario, Canada (42°34'N, 80°20'W). Situated on the north shore of Lake Erie, Long Point is a well-known stopover site for migrating *L. noctivagans* (Dzal et al. 2009; McGuire et al. 2011). For seasonal comparisons, T_a (± 0.1 °C) was recorded from an Environment Canada weather station at Long Point (42°34'N, 80°20'W). At my study site T_a are on average 10.8 °C cooler during the spring migratory period (April – May, 9.5 ± 1.6 °C) than in the autumn (August – September, 19.7 ± 1.4 °C; 20-year average, 1995 – 2015).

I captured bats using mist nets during the spring migration (April – May) in 2013 and 2014. I recorded body mass using a digital balance (± 0.1 g). Female bats were palpated to determine pregnancy status, but none were at a stage where pregnancy could be confirmed. In 2014, fat stores of live bats were measured using a quantitative magnetic resonance (QMR) body composition analyzer (EchoMRI-B; Echo Medical Systems, Houston, TX, USA) – a minimally invasive technique that measures dry fat mass and wet lean mass. QMR measurements are taken by placing an unrestrained bat in a small ventilated tube, which is then inserted in the bore of the QMR machine for three replicates of a 2-minute scan (for details see McGuire and Guglielmo 2010).

4.3.1 Radio-telemetry

In 2014, torpor expression of free-ranging bats was monitored using temperature-sensitive radio transmitters which were used to both locate bats and monitor their skin temperature (T_{sk} ; ± 0.1 °C; BD 2XT, Holohil Systems Ltd., Carp, Ontario, Canada). Transmitter pulse interval encodes the T_{sk} data (pulse intervals decrease at warmer temperatures) and signal strength is used to locate the individual. Transmitters were affixed to a small fur-trimmed area (< 1 cm²) on the mid-dorsal region using non-toxic latex adhesive (Osto-Bond, Montreal Ostomy, Quebec) that wears off within approx. 30 days. T_{sk} is considered a good indicator of core body temperature (T_b) in bats; T_{sk} is ~ 2 °C below T_b over a wide range of T_b (5 – 40 °C) (Audet and Thomas 1996; Barclay et al. 1996; McKechnie et al. 2007). Transmitters weighed 0.38 – 0.42 g and bat body mass ranged from 9.0 – 12.6 g. So transmitters ranged from 3.0 – 4.6 % of body mass, below the 5 % guideline for bats, suggested to prevent reductions in maneuverability and foraging efficiency (Aldridge and Brigham 1988). Before use, radio transmitters were calibrated in a precision water bath (Lauda Eco, LAUDA-Brinkmann, Delran, New Jersey, USA) to the nearest 0.1 °C, over a range of temperatures (1.5– 40.0 °C) against a digital thermometer (Total-Range Digital Thermometer, VWR, Radnor, Pennsylvania, USA). Following transmitter attachment, bats were held for 10 minutes to allow the glue to set and were released at the capture site.

Shortly after dawn I radio-tracked bats to their day roost using handheld antennas (3-element, Yagi) and receivers (SRX 600, Lotek Wireless Inc, Newmarket, Ontario, Canada). All T_{sk} measurements took place on the first day of data collection because all but one bat departed the study site after a single day. T_{sk} was recorded every ~ 10 seconds using custom-built data-logging SensorGnome receivers (www.sensorgnome.org) equipped with one 3-element Yagi antenna, receivers were left near the roost until the bat departed. The receiver deployment file was programed to record pulses that were shorter than 23 ms, within 0.048 MHz of the tag frequency, and at least 3 dB above background noise (Supplementary Materials). Receivers recorded radio pulse signal strength and a timestamp. The raw data were filtered by frequency offset to remove harmonics. Hampel filters with a moving window of 20 recordings were used to further

remove noise in frequency offset using the *hampel* function of the *pracma* package (v 1.9.3) in R. Following this filtering, the pulse interval between concurrent recordings was calculated. A second *hampel* filtering removed outliers in the pulse interval. Following this the individual calibration curve for each transmitter was used to convert pulse interval into T_{sk} . To delimit when a bat entered torpor, I used a T_{sk} torpor onset threshold calculated using equation 4 from Willis (2007):

$$(1) \quad T_{b-onset} - 1 - SE = (0.041)\text{body mass} + (0.040)T_a + 31.083$$

To account for the difference between T_{sk} and T_b , 2 °C was subtracted from $T_{b-onset}$ to create $T_{sk-onset}$ (Barclay et al. 1996). In this calculation T_a was the mean T_a for the duration that the bat was observed. A bat was considered torpid whenever T_{sk} dropped below this threshold. Torpor onset ranged from 29.9 – 30.4 °C for different individuals. Torpor bout duration was calculated as the cumulative time spent below the torpor onset threshold from time of first location until sunset. Autumn torpor and body composition data was taken from supplementary table 2 (McGuire et al. 2014), which used similar methods.

I monitored roost T_a by placing a temperature data-logger (HOBO Pendant, Onset, Cape Cod, Massachusetts) as near as possible to the bats, within 5 m of the roost and in the shade. When bats roosted in woodpiles the data logger was placed ~40 cm deep into an adjacent gap in the logs.

4.3.2 Respirometry

In 2013, I used flow-through respirometry to determine bats' latency to enter torpor. Torpor entry was obvious and defined as a sharp drop in O_2 consumption. Bats were held in cloth bags upon capture to await their respirometry trials which took place during the inactive period, from dawn until sunset. Bats were weighed and then placed inside 1.12L respirometry chambers made of metal canisters, which contained a hanging mesh for bats to roost upon. Respirometry chambers were housed within a temperature-controlled cabinet (± 0.2 °C; model PTC-1 with PELT-5 temperature controller; Sable Systems, Las Vegas, NV, USA) set to 10 °C. Outside air was pumped through a drier (PC-4 Peltier Effect Dryer; Sable Systems), and two columns of Drierite to remove any water vapor. Dry air was then passed through needle valves (air flow manifold MF-8; Sable Systems),

which split the flow to supply the three airtight chambers and a line used as a baseline. Flow supplied to each chamber was 250 ml/min, but in a few cases dropped as low as 120 ml/min due to difficulties with water condensing in the incurrent line. I used a multiplexer (MUX flow multiplexer; Sable Systems) to monitor each chamber for 10 min before switching to the next chamber, after all chambers were monitored I measured a baseline airflow. Between 1 and 3 bats were monitored during a trial, therefore the measurement error in latency to enter torpor could be as much as 40 min. Excurrent air was dried with a column of Drierite to remove any moisture added by subjects. Flow from each chamber was monitored with a mass flow meter (840L; Sierra Instruments, Monterey, CA, USA) and subsampled at 90 mL min⁻¹ (Gas analyzer sub-sampler v2.0 Sable Systems). Subsampled air was then sent to CO₂ (model CA-2A; Sable Systems) and O₂ analyzers (model FC-1B; Sable Systems). All readings were recorded using an analog-to-digital converter (UI-2; Sable Systems). Upon completion of the trial at sunset bats were weighed again.

4.3.3 Analysis

For free-ranging bats, linear models were used to assess effects of T_a , sex, season, fat mass, and the total time the bat was observed, on torpor bout duration, minimum T_{sk} , and $T_{sk}-T_a$. As the effect of T_a on torpor bout duration appeared non-linear, a quadratic model was also fit to the data, but this model did not have significantly better fit than the linear model (data not shown). For respirometry trial data, I used student's T-tests to compare the bats' latency to enter torpor, and mass loss between male and female bats in the experimental trial at 10 °C. Numerical values are reported as means \pm SD. Statistical analysis were conducted in R (version 3.2.4, R Core Development Team, 2016).

4.4 RESULTS

4.4.1 Spring torpor expression – free ranging bats

I outfitted 23 spring migrants with radio transmitters. Data were collected from 20 bats (N=10 male; N=10 female) and a total of 19.79 bat days of data were recorded. Bats were located at their day roosts 2.1 ± 1.4 h after sunrise. Temperature monitoring encompassed

$85.5 \pm 9.8\%$ of the daytime period (sunrise to sunset). At sunset, bats usually departed their roosts and were not found within the study area again. Five days of data were recorded from one male bat that remained in a roost during cool weather.

All bats entered torpor for the majority of the daytime (10.8 ± 2.2 h). Half of the bats had already entered torpor by the time I located them ($N = 9/20$). Ten bats remained in deep torpor (T_{sk} below 20°C) for the entire day (Fig. 4.1A). The second most common pattern was a bout of torpor in the morning and afternoon, with a single period of euthermia during the warmest part of the day (Fig. 4.1B). Three bats did not arouse from torpor at dusk, and roost T_a at sunset was between $10.6 - 15.0^\circ\text{C}$ on these nights.

Bats spent more time in torpor on days with colder mean $T_{a \text{ roost}}$ ($P = 0.02$; $R^2 = 0.31$; $F_{2,17} = 5.17$). After the effects of $T_{a \text{ roost}}$ and the total time the bat was observed were accounted for, there was no detectable effect of sex or fat mass on torpor bout duration ($P > 0.05$). Fat mass of radio-tagged bats was 0.98 ± 0.36 g fat or 8.9% of body mass. Bats maintained T_{sk} $3.9 \pm 2.1^\circ\text{C}$ above $T_{a \text{ roost}}$, and there was no effect of sex or fat on $T_{sk} - T_{a \text{ roost}}$ ($P > 0.05$). Minimum T_{sk} of torpid bats was $15.6 \pm 4.0^\circ\text{C}$ and did not differ between sexes or by fat ($P > 0.05$).

4.4.2 Spring torpor expression – respirometry trial

I experimentally tested the time since the beginning of the respirometry trial (dawn) until torpor entry for 18 bats (male $N = 6$, female $N = 12$) exposed to a T_a of 10°C . Four bats roosted on the bottom of the chambers and were damp with urine at the end of the trial, these bats were removed from further analysis (male $N = 1$, female $N = 3$). In two bats O_2 consumption was not monitored because of an error with multiplexer control file, but I was still able to record change in mass (male $N = 1$, female $N = 1$). Time until torpor entry varied from 2.25 to 9.1 h and tended to be longer in females than males, but this difference was not significant ($t_9 = 1.5$, $P = 0.17$; Fig. 4.2). Bats weighed 10.8 ± 1.5 g upon

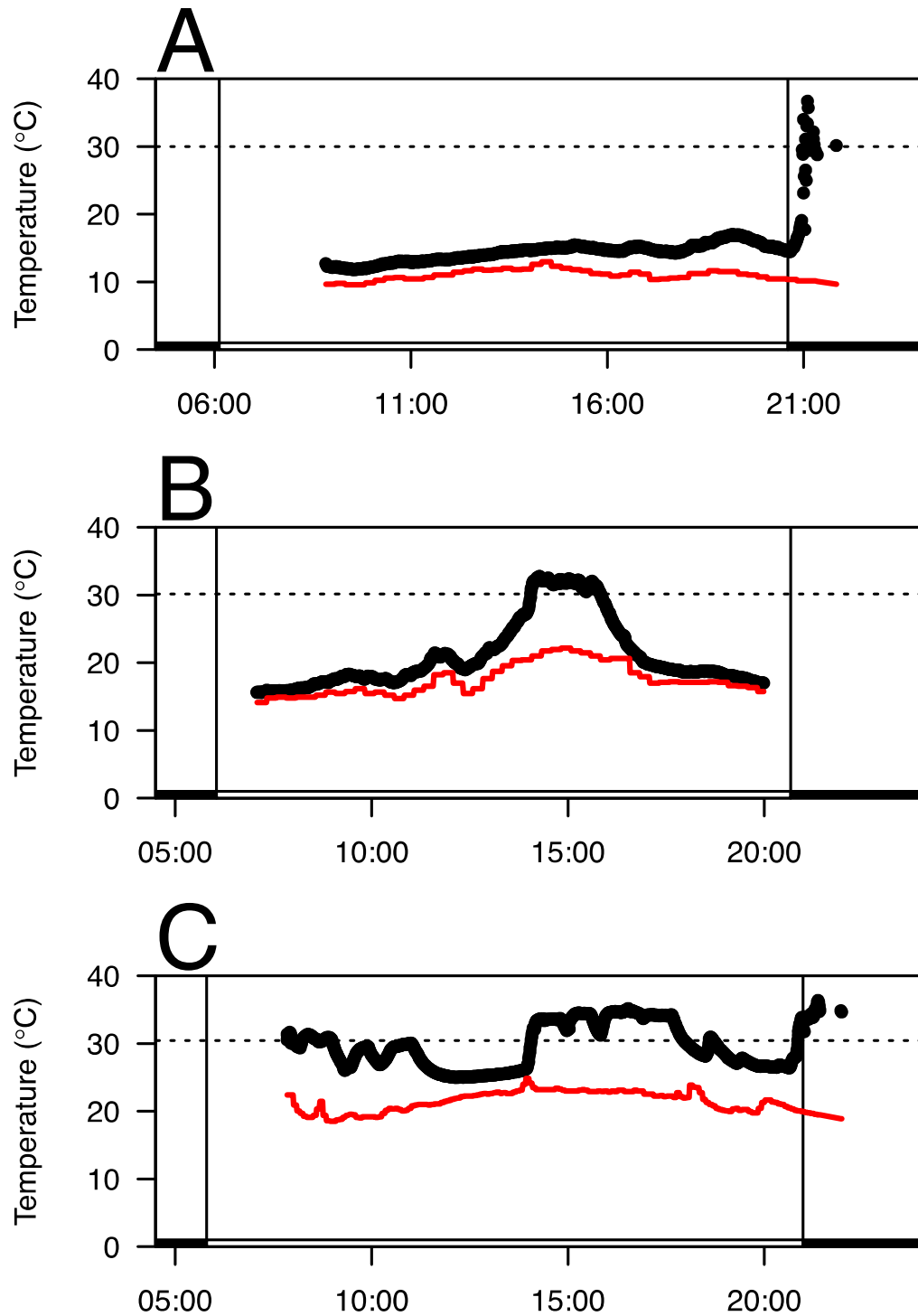


FIG 4.1– Example skin temperature (T_{sk}) traces (thick black line) of three free-ranging *L. noctivagans* (A-C). T_a denoted by thin red line. Bats were considered torpid when T_{sk} dropped below the torpor threshold (dashed line). Black bars at the bottom of figures represent periods of night with vertical lines indicating sunrise and sunset.

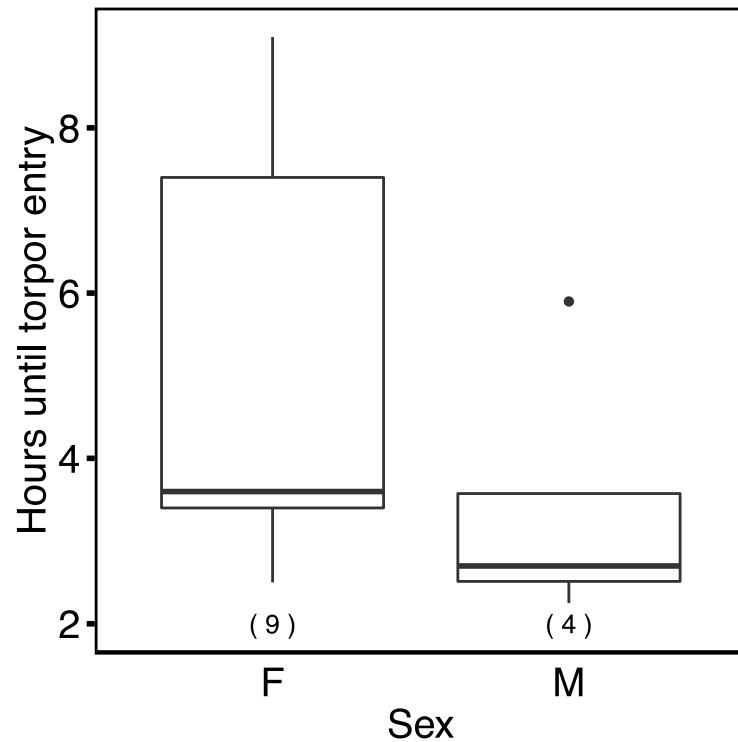


FIG 4.2– Time since beginning of respirometry trial until torpor entry of *L. noctivagans* held at an experimental temperature of 10 °C. Females tended to delay torpor entry longer than males, but this difference was not significant ($P > 0.05$). Distribution of data is shown using Tukey's box plots. Boxes designate the interquartile range, between the first and third quartiles and containing 50% of the observations, and are divided by the median. Whiskers connect boxes to the extreme points within 1.5x the interquartile range and points outside this range are individually plotted.

beginning of their respirometry trial. The decline in body mass after the trial was 2.5 fold greater in females (1.15 ± 0.81 g) than in males (0.43 ± 0.13 g; $t_{10} = 2.76$, $P = 0.02$).

4.4.3 Spring vs. autumn torpor expression

Temperatures at my study site as measured by the Environment Canada weather station were on average 11.4 °C colder, as well as more variable during the spring 2014 (this study), than they were during autumn 2011 study period (McGuire *et al.* 2014; Table 4.1). Bats entered torpor for 4.7 h more during spring (10.8 ± 2.2 h) than during autumn (6.1 ± 3.5 h). Torpor bout duration was negatively correlated with T_a ($R^2 = 0.61$, $P < 0.001$; Fig. 4.3). After accounting for the effects of T_a and observation time, spring migrants still spent 14% more time in torpor than autumn migrants ($F_{1,31} = 2.1$, $P = 0.049$; Fig. 4.4B), and females spent 14% less time in torpor than males ($F_{1,31} = 2.5$, $P = 0.017$; Fig. 4.4A; full model: $F_{5,31} = 20.5$, $P < 0.001$). Controlling for the effects of sex, season and observation time, bats with larger fat stores tended to spend less time in torpor, although this effect was not statistically significant ($F_{1,31} = 1.8$, $P = 0.08$).

Table 4.1– Ambient temperature (°C) from the Environment Canada weather station at Long Point (42°34'N, 80°20'W) during this study (spring 2014) and previous work in autumn 2011 (McGuire et al. 2014).

T _a	April – May 2014	Aug – Sept 2011	
Daily mean	8.76	20.14	$P < 0.001$
SD of daily mean	4.68	3.32	-
Mean daily min	1.61	17.99	$P < 0.001$
Mean daily max	9.64	22.36	$P < 0.001$

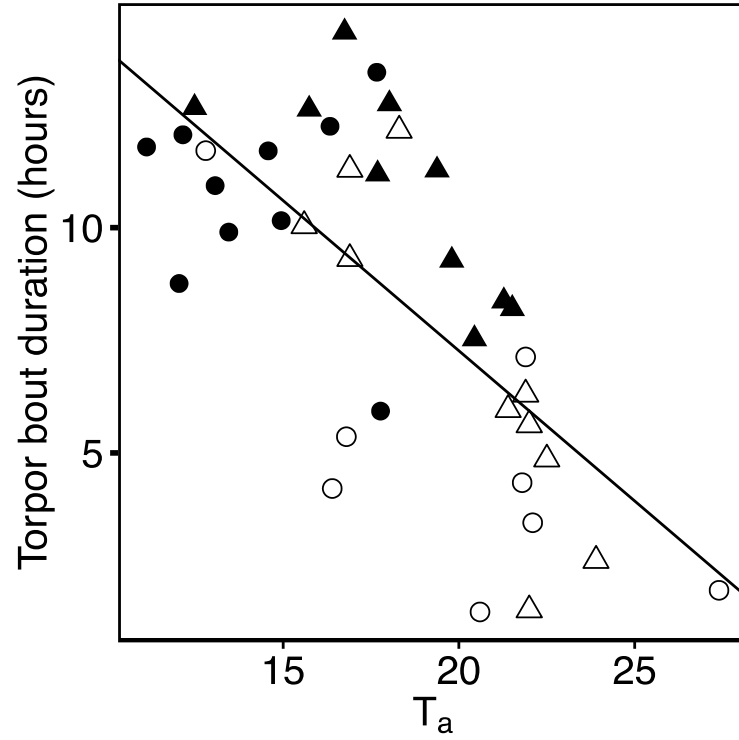


FIG 4.3– Bats spent more time in torpor at cooler T_a ($R^2=0.61$, $P < 0.001$). Autumn migrants (open symbols; data from McGuire et al. 2014) used less torpor for a given T_a than spring migrants (closed symbols; this study). Females (circles) used shorter torpor bouts than males (triangles).

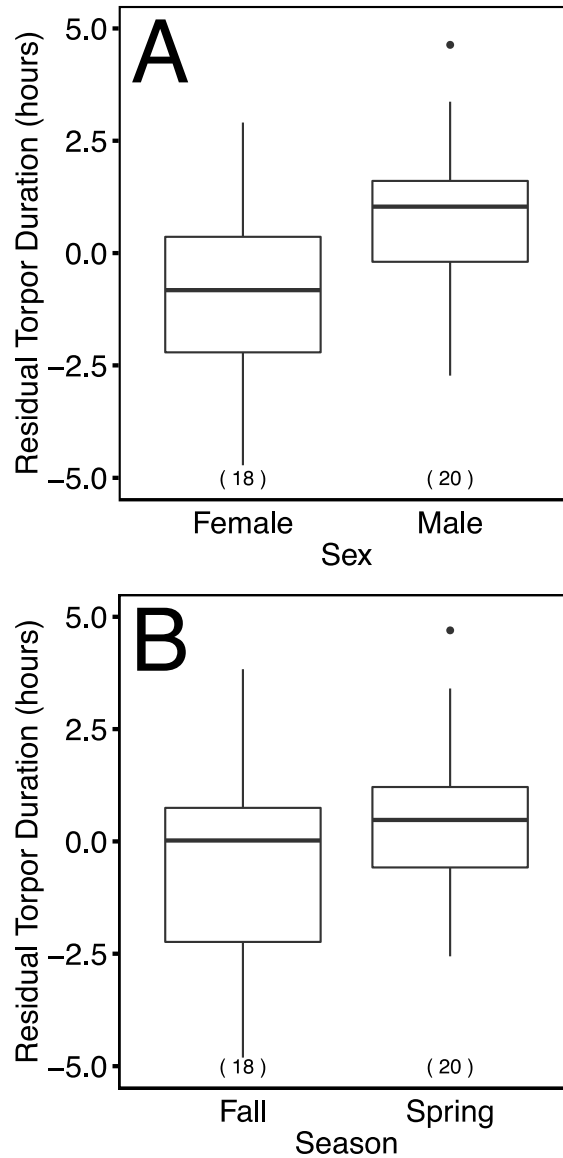


FIG 4.4—Time in torpor of free-ranging *L. noctivagans* after controlling for the effects of T_a and observation time on torpor bout duration (hours), these are the residuals from the regression in Fig. 4.3. Male bats spend more time in torpor than females (A), and spring migrants have longer torpor bouts than autumn migrants (B). Distribution of data is shown using Tukey's box plots. Boxes designate the interquartile range, between the first and third quartiles and containing 50% of the observations, and are divided by the median. Whiskers connect boxes to the extreme points within 1.5x the interquartile range and points outside this range are individually plotted.

4.5 DISCUSSION

Facultative use of torpor appears to be an important component of the migratory strategy of *L. noctivagans* in both spring and autumn. Bats used torpor extensively during both migration seasons. Further, torpor expression varied with both season and sex – spring migrants had longer torpor bouts than fall migrants and females had shorter torpor bouts than males in both seasons.

4.5.1 Season

L. noctivagans used torpor for 1.8 fold more time in spring than in the autumn. Colder spring T_a can explain a large proportion of the variation in torpor expression, but even after the effects of T_a were accounted for spring migrants used torpor for 14% more time than autumn migrants. I hypothesize that differences in foraging effort, insect prey abundance or quality could explain this seasonal shift in torpor patterns. The link between food shortage and increased torpor expression is well established. Laboratory studies have demonstrated that food restriction alone can induce torpor in several taxa including marsupials (Geiser and Baudinette 1987; Song and Geiser 1997; Bozinovic et al. 2007), rodents (Lovegrove and Raman 1998; Ehrhardt et al. 2005; Brown and Staples 2010), primates, (Génin and Perret 2003; Giroud et al. 2009), and bats (Wojciechowski et al. 2007; Matheson et al. 2010). Several field studies have found correlations between food availability and torpor expression (for a review see Vuarin and Henry 2014). For example, in a post-wildfire landscape, bats decreased their use of torpor, likely in response to an associated 20-fold increase in insect abundance (Doty et al. 2016). To distinguish the effects of food resources from thermoregulatory costs, Doucette et al. (2011) examined the use of torpor by owl nightjars (*Aegotheles cristatus*) in two nearby habitats that experienced the same T_a , but differed in insect abundance – irrigated and non-irrigated desert. They found that Australian owl nightjars respond to lower food availability by entering torpor for longer periods (Doucette et al. 2011). Although I did not directly quantify insect prey during this study, aerial insect activity is linked to T_a , with lower activity at low T_a , and activity particularly drops below 10 °C (Taylor 1963). T_a at my study site was 11.4 °C cooler during spring migration (this study)

than in the previous autumn study (Table 4.1). Therefore, I expect that prey abundance is also lower during spring migration. I propose that this low spring insect abundance could explain the increased use of torpor use by spring bats, which could not be fully explained by the effect of low T_a .

Spring T_a are also more variable from night to night than in the autumn. The standard deviation in mean daily T_a , and the range of T_a experienced were greater in the spring than in the autumn. Thus insect prey is expected to also be more variable at my site in the spring as compared to the autumn. When offered unpredictable amounts of food, fat-tailed dunnarts (*Sminthopsis crassicaudata*) increase their use of torpor more than animals offered a predictable, but comparably food-restricted diet (Munn et al. 2010). Therefore, I expect that if insect availability is less predictable in the spring, it could also increase the torpor expression of bats.

In addition to differences in prey abundance and predictability, the nutritional quality of insects may differ by season. Meal quality influences torpor expression in marsupial carnivores –mulgaras (*Dasyercus blythi*) (Pavey et al. 2009). Mulgaras whose diet was comprised of a greater proportion of vertebrate prey express less torpor than those that consumed more invertebrates (invertebrates were presumed to be of lower energy content) (Pavey et al. 2009). I predict that if insects of higher energy content are available during the autumn, it could further explain why bats use torpor less frequently during the autumn.

Further experiments are needed to determine if the seasonal difference in torpor bout duration that I observed is an acclimatization effect or a short term response to diet. In a captive study of Daubenton's bat (*Myotis myotis*), environmental conditions (T_a and food availability) were more important predictors of torpor patterns than season (Wojciechowski et al. 2007). For blossom bats (*Syconycteris australis*), however, torpor was more pronounced during the summer season, when nectar availability is unreliable, even when food intake in captivity was held constant (Coburn and Geiser 1998). Which

suggests either a seasonal acclimation or endogenous rhythm controls torpor expression in blossom bats.

4.5.2 Sex differences

During both spring and autumn, free-ranging female bats used torpor for 14% less time than males. Less pronounced torpor expression by spring females would be advantageous because it is expected to speed fetal development (Racey 1973). None of the females in this study were palpably pregnant, and were likely at an early stage of pregnancy. In other bat species, the avoidance of deep torpor only began in the third trimester (Daniel et al. 2010). My observation that spring migrating female *L. noctivagans* extensively use torpor contrasts with observations of *Lasiurus cinereus* females, which are palpably pregnant and defend normothermia when cold challenged during spring migration (Cryan and Wolf 2003). *L. noctivagans* females may behave similarly in later stages of pregnancy. If this is the case, then the pace of female migrants may slow, if they use less torpor later in the migratory period.

The pattern of decreased torpor use by females was also apparent in autumn, when females are non-reproductive. Thus, factors other than pregnancy likely contribute lesser use of torpor by females. If female *L. noctivagans* have a different foraging strategy than males, it could affect their proclivity to enter torpor. I hypothesize that females forage more intensely than males to accrue sufficient fat stores to support the future costs of lactation. Experimental manipulations of meal size predicted time until torpor entry in little brown bats (*Myotis lucifugus*) (Matheson et al. 2010). Matheson et al. (2010) hypothesized that the delayed entry into torpor after foraging is an adaptation to ensure sufficient digestion and absorption of nutrients that would be impaired by torpor. Short-term responses to meal size are also hypothesized to dictate torpor expression of *S. crassicaudata* (Munn et al. 2010). Moreover, the short-term effects of meal size on torpor expression appear to apply to some free-ranging bats. Lactating big brown bats (*Eptesicus fuscus*) that foraged longer expressed shorter torpor bouts (Rintoul and Brigham 2014).

I found no sex difference in time to torpor entry in my experimental trial at 10 °C. This may be because of my relatively small sample size of males, or because as bats waited for their trial to start at dawn, they missed out on foraging time and may have finished digesting by the time the trial began. Whereas bats that were radio-tagged and released were free to resume their normal activity patterns and forage before dawn.

4.5.3 Summary

In summary, the effects of T_a could not fully explain the seasonal variation in torpor bout duration, and I hypothesize that this effect is driven by differences in prey abundance, predictability and/or quality. While I cannot exclude the possibility that pregnancy drives sex differences in torpor use in the spring, torpor expression may in part be determined by differences in the foraging effort of males and females. If the torpor variation I observed is driven by meal size, my data suggest that females forage more intensely than males during both spring and autumn migrations. No data on the refueling rates or pace of migration exist for *L. noctivagans*, so it is difficult to determine if the additional use of torpor in spring is sufficient to compensate for presumed lower foraging opportunities during the spring, or if food availability and T_a are limiting for the pace of spring migration. Ongoing work at our site is examining seasonal differences in insect abundance and energy content. Future work should examine the relative foraging effort of spring and autumn migrants. Further study is required to determine if torpor use is enhanced during the migration as compared to pre-migration.

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CHAPTER 5

SPRING AND AUTUMN MIGRATORY MOVEMENTS OF NORTH AMERICAN TREE-BATS (*LASIONYCTERIS NOCTIVAGANS*, *LASIURUS BOREALIS* AND *LASIURUS CINEREUS*) MEASURED USING THE MOTUS WILDLIFE TRACKING SYSTEM

5.1 ABSTRACT

Lack of knowledge about the behaviour of migratory species during the migratory period is a major barrier to conservation efforts. This is especially true of North America's tree-roosting bats: *Lasiurus cinereus*, *Lasiurus borealis*, and *Lasionycteris noctivagans*. We used the Motus wildlife tracking system, an array of 72 radio receiving towers situated in south-western Ontario, Canada to follow the movements of 65 migrating bats during both spring and autumn. We provide the first long distance movement tracks and estimates of migration speeds of North American tree-bats. We found no evidence that bats were preferentially following leading lines of features oriented primarily north to south (shorelines of Lake Huron or the Niagara escarpment), although several bats moved along the shoreline of Lake Erie which runs east to west. Autumn migrating *L. noctivagans* traveled through the monitored space at an average speed of 133 ± 112 km per day, much less rapid than their estimated ground speeds of 50 ± 19 km h⁻¹ should allow. This strongly implies that bats are using stopover periods and are selective regarding when to move.

Keywords: automated radio-telemetry, Chiroptera, flight speed, leading lines, flight behaviour, migration corridor, migration speed, migration route, tailwind assistance, wind energy

5.2 INTRODUCTION

One of the greatest barriers to effective conservation and management of migratory animals is our ability to determine the importance of various landscapes and how they are used throughout the year (Wilcove and Wikelski 2008). The ecology of North America's migratory, tree-roosting bats (*Lasionycteris noctivagans*, *Lasiurus borealis*, and *Lasiurus cinereus*) is very poorly known, and even less is understood about the behaviour and habitat requirements of these species during migratory periods. High incidence of migratory bat mortality at industrial wind energy facilities is a cause for concern. Between 2000 and 2011 an estimated 650,104 to 1,308,378 bats, mainly migratory tree-bats, were killed at industrial-scale wind turbines in Canada and the United States (Arnett and Baerwald 2013). The impact of this mortality on populations is difficult to assess because good population estimates are lacking, but they may be substantial enough to threaten population viability (Frick et al. 2017).

This conservation threat has provided impetus to answer fundamental questions about the basic biology of migratory bats (Arnett et al. 2016). For example, how do landscape features shape movement? Identification of key landscape features could help regulators to delineate migration corridors and that should be taken into account when constructing wind energy facilities (Arnett et al. 2016). Are there behavioural differences between spring and fall migration? Understanding what, if any variation occurs in migratory routes between seasons may allow us to better manage and mitigate bat fatalities at wind energy facilities. The vast majority of wind-turbine mortality has been reported during the autumn migration period. Few mortalities have been reported in the spring. Although hypotheses have been proposed to explain the differential mortality, such as the mate attraction hypothesis – that bats congregate near the tallest structures on the landscape in the autumn to facilitate mate searching, the cause is still unknown (Cryan and Barclay 2009).

Migratory movements of tree-bats have been inferred from visual (Cryan and Brown 2007) and acoustic (Baerwald and Barclay 2009; Furmankiewicz and Kucharska 2009; Hooton 2010; Johnson et al. 2010; Cryan et al. 2012; Hamilton 2012) surveys, mortality

at wind energy facilities (Arnett et al. 2008; Baerwald and Barclay 2009), and analysis of museum collections (Cryan 2003). In birds, large-scale mark-recapture efforts have provided a wealth of information about movement patterns and survival rates. Banding of tree-bats has been largely ineffective because these species are elusive, and they are generally solitary or form small colonies (< 40 individuals). Tree-bats are difficult to band in large numbers and the relative scarcity of bat researchers (as compared to bird banders), make recaptures extremely unlikely. Stable isotope analysis of bat fur has been used to estimate migration distances and connectivity between habitats (Cryan et al. 2004; Fraser et al. 2012; Voigt et al. 2012; Baerwald et al. 2014).

Banding and stable isotope analyses provide a snapshot of bat activity at fixed locations, but cannot provide data about individual movements. None of the methods described above currently have the precision to delineate migration corridors, and intensive survey efforts are needed to identify stopover habitats (Hooton 2010). Small body size of most insectivorous bats prohibits them from carrying GPS tags – the “small animal problem” (Holland and Wikelski 2009; Bridge et al. 2011). Geolocators, although lighter than GPS tags (0.5 g), rely on the timing of sunrise and sunset, and are ineffective for nocturnal species that spend the day roosting in cavities or shaded by the tree canopy (Lisovski et al. 2012). Recent advances in the miniaturization of radio transmitters now allow very small species, weighing as little as 4 g to be tracked. Radio transmitters broadcast a signal that can then be detected by a radio receiver tuned to the appropriate frequency. A drawback of radio telemetry tracking is that receivers must be within range to detect the radio-tagged animal; researchers can easily lose contact with flying animals if they cross barriers (e.g. lakes) or leave road networks. Tracking using small aircraft can solve some of these challenges, but it remains logistically challenging to track multiple individuals concurrently. The Motus wildlife tracking system (<http://motus.org/>) is a radio-telemetry array consisting of a network of strategically placed automated telemetry receivers. Individual migrants are detected as they pass by checkpoints, allowing a large number of migrants to be tracked simultaneously. I used lightweight transmitters (0.29 g) in combination with Motus to investigate the movement ecology of individual bats as they traveled across southwestern Ontario, Canada.

My first objective was to map the migration routes of bats traversing southwestern Ontario. I hypothesized that landscape-structure influences migration routes. I predicted that topographic features, geographical barriers, and habitat types will concentrate migrating bats. Acoustic data suggest bats move along leading lines – landscape features such as mountain ranges (Baerwald and Barclay 2009), rivers (Furmankiewicz and Kucharska 2009), and coastlines (Barclay 1984). Migratory corridors for bats have not yet been identified in southwestern Ontario, but, given the geographic features in this region (e.g., the shorelines of Lake Erie and Huron, the Bruce Peninsula, the Niagara Escarpment), I predicted that such corridors exist. An acoustic study conducted in southwestern Ontario found no support for the hypothesis that bats use the Great Lake shorelines or the Niagara escarpment as migration routes, but this may be due to confounding echolocation calls from non-migrating individuals (Hamilton 2012). I further hypothesized that bats preferentially use different habitat types during different migration seasons. I predicted that during autumn migration bats select routes that incorporate features such as ridgelines that facilitate finding a mate, whereas habitats important for foraging such as riparian corridors are used more during spring migration.

My second objective was to estimate the speed of migration and flight speed of bats. Aerodynamic theory proposes that bats can fly at either their minimum power speed (V_{mp}) to minimize the amount of energy used for a unit of time, or at their maximum range speed (V_{mr}) to minimize the amount of energy used to cover a unit of distance (Hedenström and Ålerstam 1995). I hypothesized that bats would fly near their maximum range speed to travel most efficiently.

5.3 MATERIALS AND METHODS

5.3.1 Study site and capture methods

I used monofilament mist nets (mesh size 28 mm) to capture bats during migration periods. In spring, bats were captured at the base of the Long Point Peninsula, ON, Canada at the Old Cut field station of the Long Point Bird Observatory (42°34'N, 80°20'W) from April 3-May 31, 2012 and April 4-June 5, 2014. This site is previously

described in more detail in McGuire et al. (2011). I captured autumn migrating bats at the northern end of the Motus array on the Bruce Peninsula, ON, Canada (45°14'N, 81°38'W), from August 5-October 9, 2014. Because no trapping location was previously known on the Bruce Peninsula, I explored several potential netting sites: a shoreline on private property (45°13'N, 81°43'W), Little Cove (45°14'N, 81°36'W), Emmet Lake (45°13'N, 81°27'W), Singing Sands (45°11'N, 81°34'W), and the Bruce Peninsula Bird Observatory (45°14'N, 81°17'W). The northern Bruce Peninsula landscape is comprised of mature mixed forest, dominated by balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and sugar maple (*Acer saccharum*). Coastal habitats are alvars, containing slow growing eastern white cedars over 500 years in age and having a canopy height of about 9 m (Schaefer and Larson 1997). Between 5 and 18 mist-nets, ranging from 3 – 7 m in height, were opened from dusk until dawn every night, with the exception of the first two weeks of August when nets were run from dusk until 2am. Nets were not opened on nights when this was prevented by rain, high winds or ambient temperatures (T_a) below 3 °C (no bats were captured below 5 °C in the first year of the study).

Upon capture, bats were weighed ± 0.1 g using a digital scale (CS200, OHAUS, Parsippany, NJ, USA), sexed, and aged as adults or young-of-the-year using the degree of closure of the epiphyseal cartilages of the metacarpal-phalangeal joint (Kunz and Anthony 1982). We outfitted bats with radio-transmitters (NTQB-1 Lotek, Newmarket, ON) secured to a fur trimmed region on the bats' upper back using a non-toxic latex glue (Ostobond; Ostomy Quebec), which wears off in approximately 30 days. The transmitters weighed 0.29 g and bat masses ranged from 8.6 g – 30.9 g, so transmitter masses ranged from 3.4 – 0.9 % of the body mass of the bats, which is less than the accepted guideline of less than 5 % suggested to significantly decrease maneuverability and hinder foraging (Aldridge and Brigham 1988). We outfitted a total of 65 bats with radio-transmitters (Table 5.1). All research activities were approved by an Animal Use Protocol from the University of Western Ontario Council on Animal Care (protocol 2010-020; Appendix E), and were

Table 5.1– Number of radio-transmitters deployed over three migration seasons.

Year	Season	<i>Lasionycteris noctivagans</i>		<i>Lasiurus borealis</i>		<i>Lasiurus cinereus</i>	
		Male	Female	Male	Female	Male	Female
2012	Spring	11	11	1	0	0	1
2014	Spring	5	11	0	3	0	1
2014	Autumn	5	4	7	2	1	2
Total		21	26	8	5	1	4

permitted under a Wildlife Scientific Collector's Authorizations from the Ontario Ministry of Natural Resources (authorization no. 1067554 and 1076439; Appendix D).

5.3.2 Radio-telemetry array

When I began the study in spring 2012 the pilot telemetry array consisted of just eight receiving towers. By 2014 the Motus wildlife tracking system in southwestern Ontario consisted of approximately 72 towers positioned strategically across the region (Fig. 5.1). The system monitored a single radio frequency (166.380 MHz) and each transmitter emitted a unique coded identifying pulse every ~12 seconds. This allowed all bats to be monitored simultaneously, which reduced the chances of missed detections that could occur if receivers scanned different frequencies for individual radio tags. Each Motus station is composed of an automated SensorGnome telemetry receiver (www.sensorgnome.org) and three 9-element directional antennas mounted on a 6 m mast. Simultaneous detections estimate the range of these towers are up to 15 km (this study).

5.3.3 Analysis

I plotted the routes taken by bats by connecting the points between consecutive Motus stations where bats were detected. I estimated the flight speeds of migrating radio-tagged bats by observing the time taken to cross distances between Motus stations (23 – 304 km). Distance and bearing between towers were calculated using the *distHaversine* and *bearing* functions of the *geosphere* package, which take into account the curvature of the earth (Hijmans et al. 2016) in R (version 3.2.4, R Core Development Team, 2016).

Tail wind assistance was calculated at surface level and at 925 mb (approx. 750-800 m altitude), 850 mb of pressure (approx. 1500 m), and 750 mb (approx. 3000 m) using the R package RNCEP (Kemp et al. 2012). This package queries the National Centers for Environmental Prediction reanalysis data set (<http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.html>) and interpolates wind over between locations and time points. We made the simplifying assumption that bats intended bearing was a direct line between pairs of towers, and determined wind

direction and speed at the tower of origin. Tail wind assistance was calculated at the tower of origin for each pair of towers a bat moved between. Air speed was calculated by subtracting tail wind assistance at surface level from ground speed.

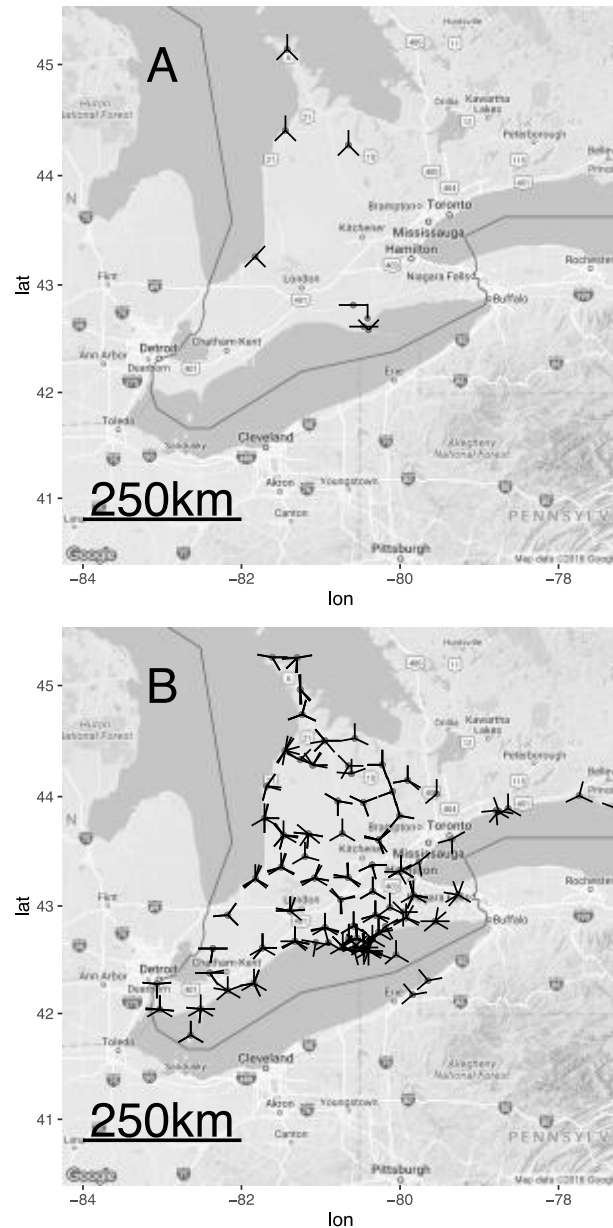


FIG. 5.1– MOTUS wildlife tracking system in a) 2012 and B) 2014. Towers are indicated by grey dots. Black lines denote antennae orientations and a 15 km estimated detection distance. When towers have more than three antennas, the antenna orientations were adjusted throughout the detection season.

N denotes number of bats and n denotes number of replicates.

5.3.4 Estimates of V_{mr} and V_{mp}

To estimate the power curve for *L. noctivagans*, I used the Pennycuick aerodynamic model (Pennycuick 2008) rather than the Norberg model (Norberg 1990) because the Pennycuick model better matches data from bats (Grodzinski et al. 2009; Suba 2014). I used the program FLIGHT V 1.24 to create the power curve and calculate minimum power speed and maximal range speed (available from

<http://www.bristol.ac.uk/biology/people/colin-j-pennycuick/research.html/>).

Morphometric data required for the model were taken from (Farney and Fleharty 1969) and represents 35 individuals: wingspan (289.37 mm) and wing area (114.98 cm²). For mass I used the average of individuals in this study (10.5 g). Altitude was set at 250 m above sea level, the elevation of Long Point.

5.4 Results

5.4.1 Spring movements

In spring 2012 I was able to track two *L. noctivagans*, and in 2014 I was able to track eight *L. noctivagans*, two *L. borealis*, and one *L. cinereus* traveling beyond the capture site (Table 5.2). In 2012, 20 *L. noctivagans*, one *L. borealis* and one *L. cinereus* were not detected at towers outside of the capture site. In 2014, eight *L. noctivagans*, and one *L. borealis* were not detected at towers outside of the capture site. Routes taken by bats departing from Long Point did not indicate a clearly defined migratory corridor, and there was no evidence of travel either along the shoreline of Lake Huron or the Niagara Escarpment (Fig. 5.2).

Silver-haired bats.— Five *L. noctivagans* headed northwards while the remaining five traveled along the shoreline of Lake Erie. Of the five bats that travelled along the shoreline, four departed eastward off the tip of Long Point and were not subsequently re-detected within the array. The other bat traveled about 110 km west along the shoreline.

Table 5.2– Summary of spring movements

Tag ID	Species	Sex	Distance (km)	Number of days	Estimated average migration speed (km/d)
126	<i>L. noctivagans</i>	Male	221	10.1	22.1
95	<i>L. noctivagans</i>	Female	355	2.9	105.9
379	<i>L. noctivagans</i>	Female	251.4	14.6	17.2
382	<i>L. noctivagans</i>	Female	189.3	2.3	82.1
386	<i>L. noctivagans</i>	Female	147.7	11.6	12.7
390	<i>L. noctivagans</i>	Male	109.0	2.0	52.5
405	<i>L. noctivagans</i>	Female	28.9	2.9	10.0
407	<i>L. noctivagans</i>	Female	28.9	4.8	6.0
408	<i>L. noctivagans</i>	Male	28.9	7.9	3.7
410	<i>L. noctivagans</i>	Female	28.9	2.1	23.8
413	<i>L. cinereus</i>	Female	371.9	6.2	60.0
381	<i>L. borealis</i>	Female	176.3	1.2	146.0

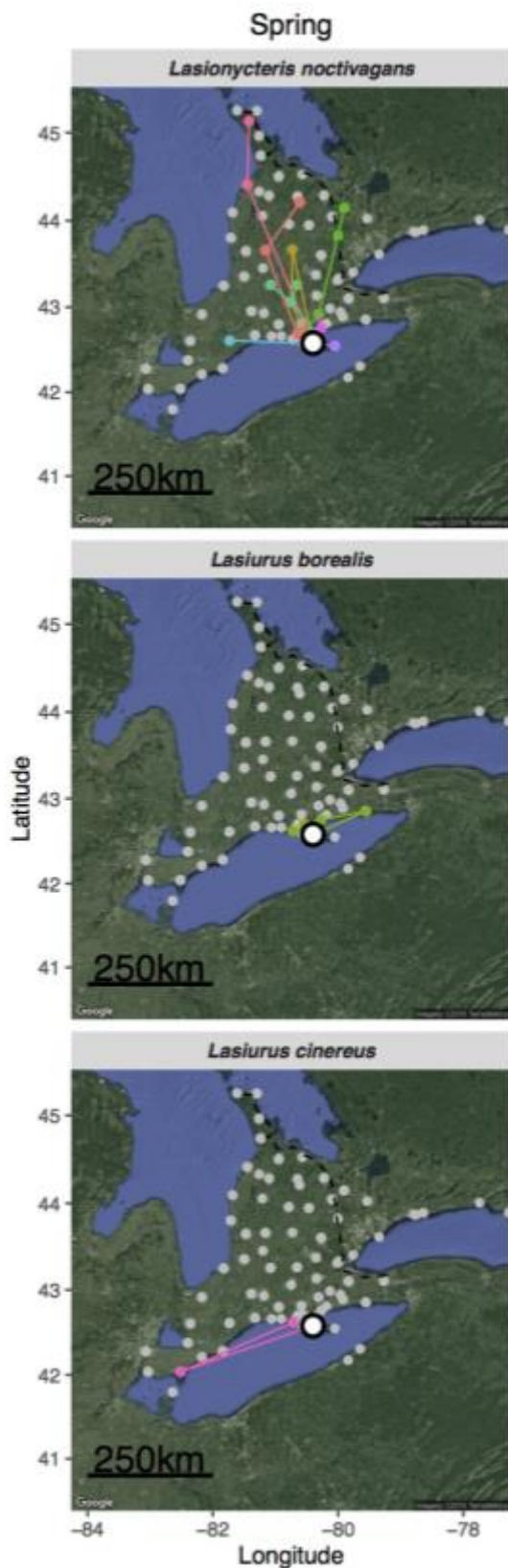


FIG. 5.2– Spring migration tracks of bats in 2012 and 2014. Capture sites are indicated by an open circle. Grey circles denote MOTUS tower locations. Coloured circles represent tower detections for individual bats and lines connecting them are the shortest paths between towers. Dashed line denotes the Niagara escarpment.

Eastern red and Hoary bats.— One *L. borealis* traveled eastwards from Long Point, before nearly returning to the capture site 1.2 days later, a 176 km round trip. A second *L. borealis* remained near the capture site and was redetected for 10 d at a receiver tower 18 km north-west of Long Point, before returning to the capture site for another 10 d. The only *L. cinereus* we captured in spring traveled southwest to Point Pelee and returned to the capture site in a loop that took 6.2 nights and covered at least 370 km (Appendix, Bat 413).

5.4.2 Autumn movements

In autumn I was able to track nine *L. noctivagans*, four *L. borealis*, and two *L. cinereus* traveling beyond the capture site (Table 5.3). Three *L. borealis* were not detected at towers outside of the capture site. Routes taken by bats departing from the northern terminus of the Bruce Peninsula did not indicate a clearly defined migratory corridor, although some individuals appeared to travel along the Niagara Escarpment (Fig. 5.3).

Silver-haired bats.— I tracked nine *L. noctivagans* in autumn for an average distance of 288 ± 56 km for between 1.0 - 32.9 days (Table 5.3). The average pace of movement was 133 ± 112 km per day (range 9 – 281 km per day). Four bats followed a central trajectory traveling nearly due south from the tagging site. Three bats moved in a south-eastern direction, co-incident with the line of the Niagara Escarpment. One bat was not detected within most of the array, but later was detected far to the south west at Lake St. Clair; the route taken cannot be determined (Fig. 5.3).

Eastern red bats.— Four *L. borealis* were observed traveling southwards from the Bruce Peninsula, not following the shoreline or the Niagara Escarpment (Fig. 5.3). Three red bats were not detected leaving the capture site, and remained for 6 - 50 days.

Hoary Bats.— All tagged *L. cinereus* were detected until they departed the study region. One first year female hoary bat traveled southwest, moving along the Lake Huron shoreline and arriving at Lake St. Clair. The other *L. cinereus* (an adult male) took a

Table 5.3– Summary of autumn movements

Tag id	Species	Sex	Age	Distance (km)	Total time (d)	Estimated average migration speed (km/d)
256	<i>L. noctivagans</i>	Female	YOY	375.1	15.1	25.2
257	<i>L. noctivagans</i>	Male	YOY	194.9	4.1	47.5
261	<i>L. noctivagans</i>	Male	YOY	290.4	32.9	8.8
505	<i>L. noctivagans</i>	Female	YOY	347.4	8.0	43.5
506	<i>L. noctivagans</i>	Male	Adult	261.2	1.4	187.1
507	<i>L. noctivagans</i>	Male	Adult	304.6	1.3	234.3
508	<i>L. noctivagans</i>	Female	YOY	260.0	1.1	236.4
509	<i>L. noctivagans</i>	Female	YOY	270.0	1.0	281.2
263	<i>L. cinereus</i>	Male	Adult	44.25	30.0	14.6
511	<i>L. cinereus</i>	Female	YOY	358.8	2.0	179.4
515	<i>L. borealis</i>	Male	Adult	161.6	2.1	76.9
517	<i>L. borealis</i>	Male	Adult	180.6	0.2	–
267	<i>L. borealis</i>	Male	Adult	419.5	9.4	46.7
268	<i>L. borealis</i>	Male	Adult	42.4	3.0	–
269	<i>L. borealis</i>	Male	Adult	228.0	25.9	–

Table 5.4– Estimated flight speeds (mean \pm SD) of bats migrating past pairs of Motus towers.

	<i>Lasionycteris noctivagans</i>	<i>Lasiurus borealis</i>	<i>Lasiurus cinereus</i>
Air speed ms ⁻¹	9.9 \pm 4.6	5.9 \pm 3.3	9.4 \pm 6.2
Ground speed ms ⁻¹	13.8 \pm 5.3	8.8 \pm 4.0	10.8 \pm 5.3

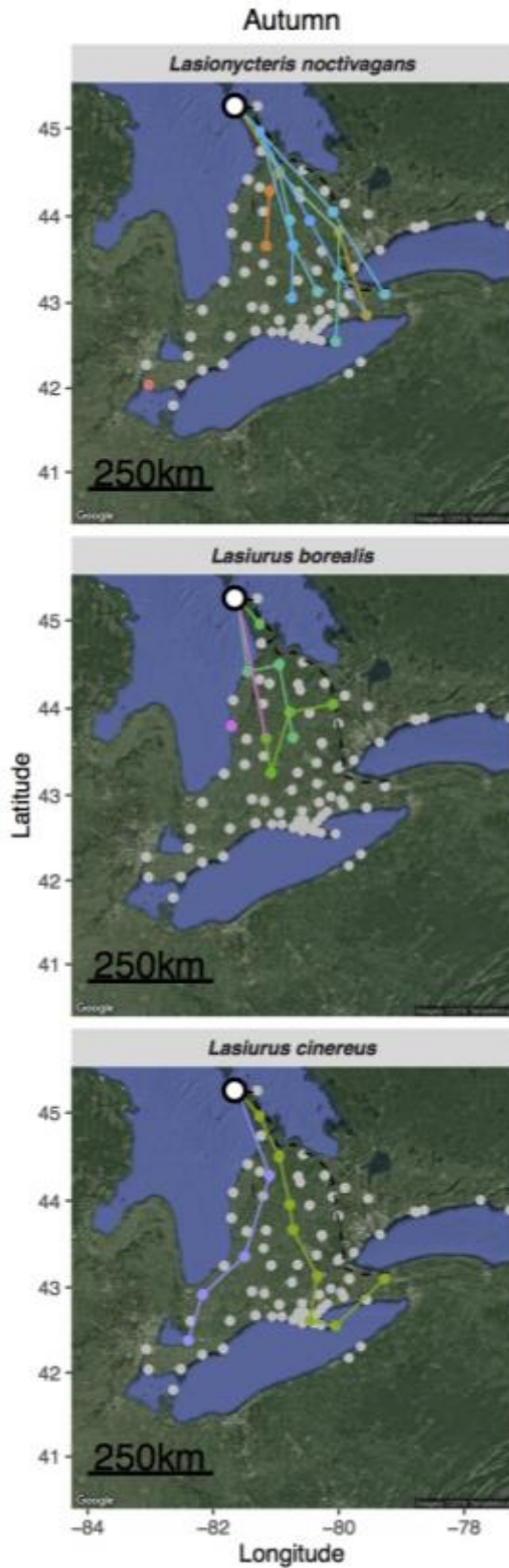


FIG. 5.3– Autumn migration tracks of bats in 2014. Capture sites are indicated by an open circle. Grey circles denote MOTUS tower locations. Coloured circles represent tower detections for individual bats and lines connecting them are the shortest paths between towers. Dashed line denotes the Niagara escarpment.

central route, traveling directly south before vanishing off the tip of Long Point. After not being detected within the array for 23 days, this male re-appeared on the southern shore of Lake Ontario (Fig. 5.3).

5.4.3 Flight speed

Enough data were available to estimate the ground and air speeds of 13 *L. noctivagans*, two *L. borealis* and three *L. cinereus* that were detected flying continuously between separate radio receiver towers. We recorded 40 individual instances of bats flying between pairs of towers. The average ground speed for *L. noctivagans* was $13.8 \pm 5.3 \text{ m s}^{-1}$ or $49.7 \pm 19.0 \text{ km h}^{-1}$ ($n = 26$), and this speed exceeded those recorded for *L. borealis* ($8.8 \pm 4.0 \text{ m s}^{-1}$; $n = 6$) and *L. cinereus* ($10.8 \pm 5.3 \text{ m s}^{-1}$; $n = 8$) (Fig. 5.4). Bats received on average $3.23 \pm 3.06 \text{ m s}^{-1}$ tailwind assistance at surface level, and accordingly air speeds were lower than ground speeds for all species (Table 5.4; Fig. 5.4). Using Penniquick's model, *L. noctivagans* estimated V_{mp} (the speed at which travel is cheapest per unit time) was 4.7 m s^{-1} , while the V_{mr} (the speed at which travel is cheapest per unit distance) was 12.5 m s^{-1} (Fig. 5.5). Our estimates of free-ranging *L. noctivagans* air speeds fell between their predicted V_{mp} and V_{mr} (Fig. 5.5).

Surface tail wind component and tail wind component at 925 mb were more strongly correlated with ground speed (surface: $R^2 = 0.20$, $p = 0.004$; 925 mb: $R^2 = 0.120$, $p = 0.004$) than at higher altitudes (850 mb: $R^2 = 0.14$, $p = 0.02$; 700 mb: $R^2 = 0.08$, $p = 0.06$).

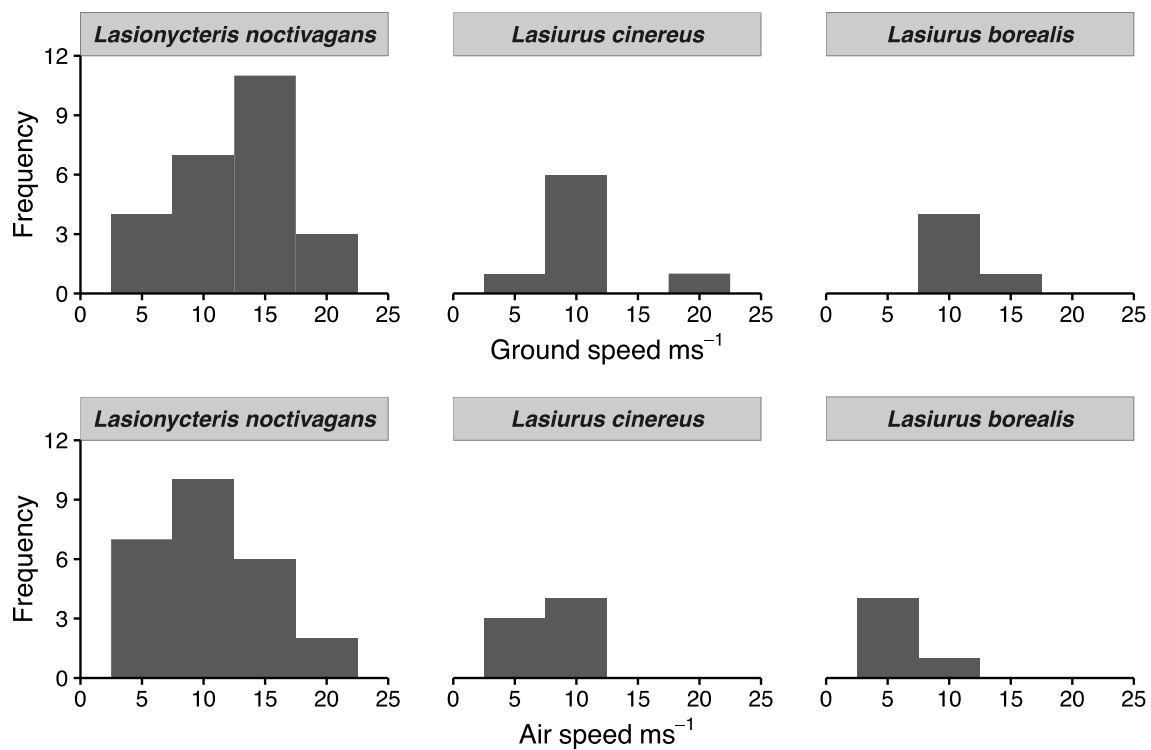


FIG. 5.4— Estimates of ground speed and air speed of migrating tree-bats taken from the time it took bats to pass pairs of towers.

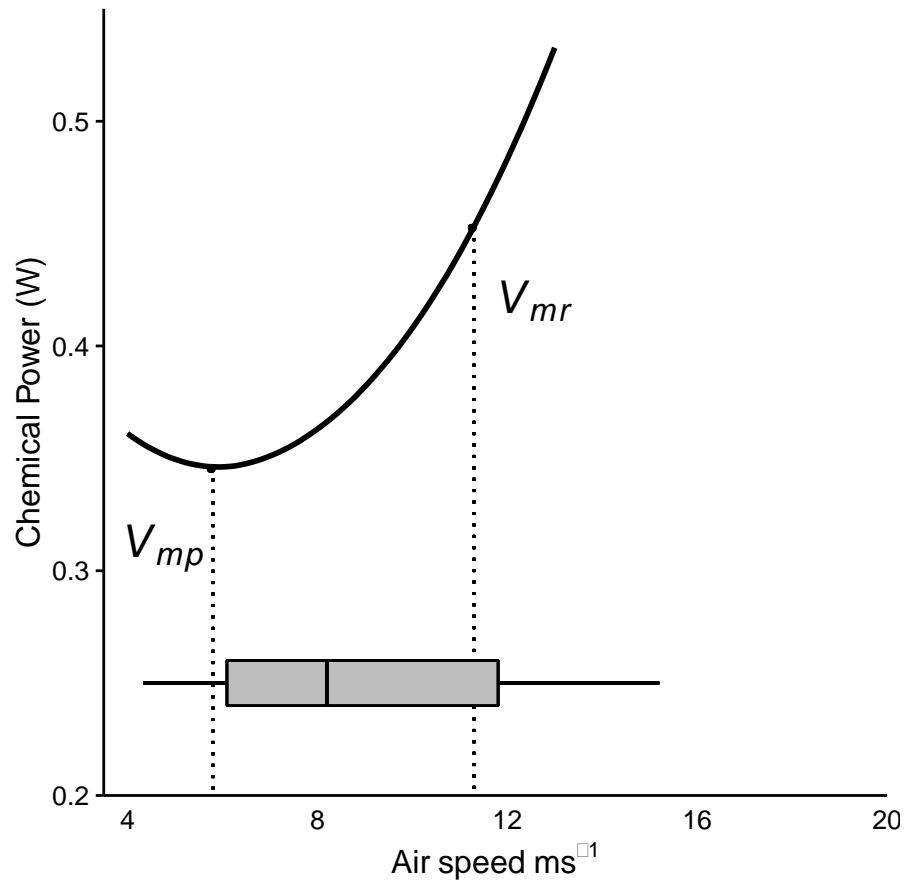


FIG. 5.5— Chemical Power curve for *L. noctivagans* showing minimum power speed (V_{mp}) and maximum range speed (V_{mr}), generated following the aerodynamic model from (Pennycuick 2008). Box plot indicates the 10th, 25th, 75th and 90th percentiles and median flight speeds of migrating bats from both migration seasons.

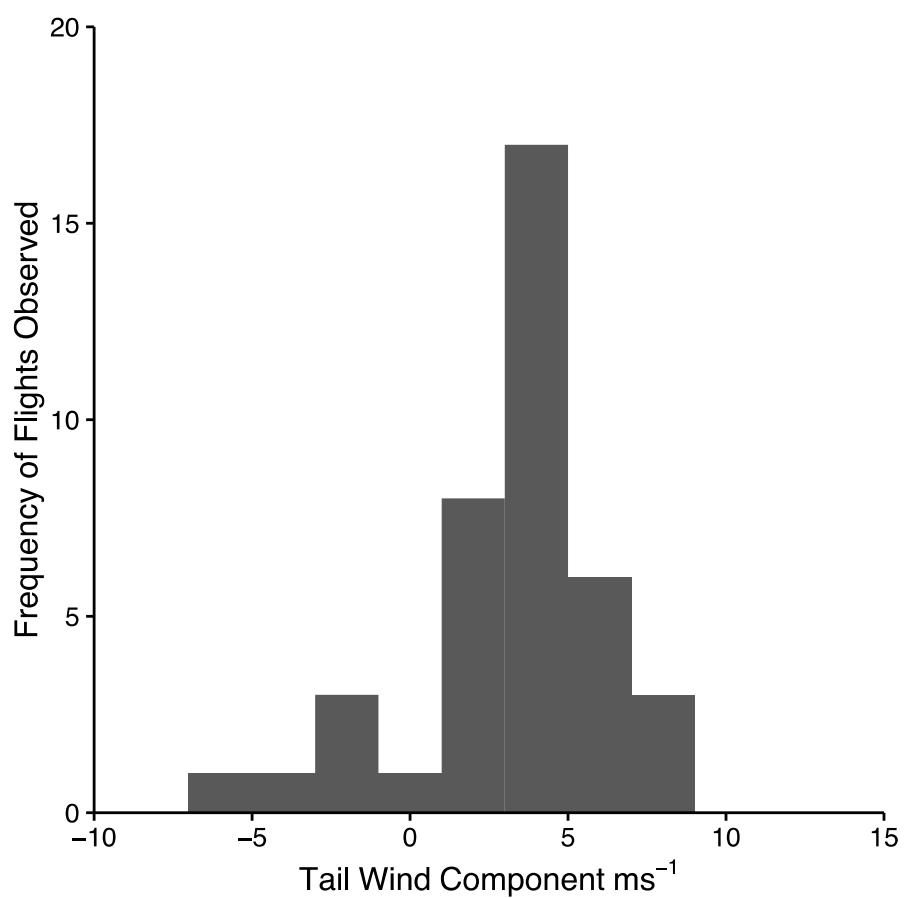


FIG. 5.6—Tail wind component at ground level of bats making migratory flights.

5.5 Discussion

I provide the first continuous long distance movement tracks of individual migrating bats in North America, and demonstrate the utility of the Motus wildlife tracking system to map migratory pathways of bats. These detailed data on the movements of individual bats have been difficult to measure previously because of the small animal problem – transmitters light enough to attach to small animals have a limited detection range (Wikelski et al. 2007). We addressed this challenge by using a combination of lightweight transmitters (0.29 g) and increasing detection probability by using an array of radio-receiving stations rather than following individuals. This method has allowed us to gain unprecedented insight into how migrating bats move across the landscape.

5.5.1 Migration Routes

The routes taken by migrant bats varied broadly by species and individual. We found no evidence that bats preferentially travelled along the north to south running shorelines of the Great Lakes or along the Niagara Escarpment. During spring migration, the most important movement corridor appeared to be the shoreline of Lake Erie, bats of all species made both eastward and westward movements along this shoreline. As bats are traveling north from the north shore of Lake Erie in the spring, the lake does not act as a barrier at this point. Lakeshores and associated wetlands may be profitable foraging grounds for emergent insects. Northward movement followed a dispersed, broad front pattern. In autumn, a broad south-east migration corridor appears to exist along the Niagara escarpment for *L. noctivagans*. Long Point is a well-known stopover site for *L. noctivagans* (Dzal et al. 2009; McGuire et al. 2011; 2014), but none of the fall migrants tagged in our study passed through Long Point. This trajectory suggests that bats stopping over at Long Point originate from elsewhere.

5.5.2 Flight speed

The observed migration air speed of *L. noctivagans* ($9.9 \pm 4.6 \text{ m s}^{-1}$) was double the values previously reported for this species in a flight course (5.0 m s^{-1}) (Hayward and Davis 1964). The use of flight speeds approximating V_{mr} is seen in the commuting flights of *Pipistrellus kuhlii*, but interestingly these bats switch to a flight speed closer to the minimum power speed (V_{mp}) when foraging (Grodzinski et al. 2009). Optimal migration theory suggests that migrants can fly at V_{mr} to minimize energy, or above V_{mr} to minimize time (Alerstam and Lindström 1990) if taking into account stopover time losses. Air speeds exceeding V_{mr} have been reported for several passerine birds smaller than 0.1 kg, and may indicate that minimization of total time on migration is more important than energetic concerns for many birds (Welhun 1994). *L. noctivagans* air speeds fell short of their predicted V_{mr} (11.3 ms^{-1} ; Fig. 5.6), which suggests one of two possibilities. First, bats flew at or above their V_{mr} , but their perceived flight speeds were reduced because the path bats took between the pairs of Motus towers was not a direct route. Or second, bats flew at an intermediate speed which falls between a time and energy minimization strategy, spending part of the night using foraging flights in the direction of travel and the remainder undertaking rapid migratory flight. Migrating *Pipistrellus nathusii* appear to travel more quickly than their predicted V_{mr} , which would argue for the first option but this study failed to compensate for wind assistance (Suba 2014). Therefore, I suggest that *L. noctivagans* have high speed direct flights, but that they might stop for brief feeding or drinking along the way, particularly if bats migrate at low altitudes.

The values of *L. borealis* and *L. cinereus* flight speeds should be taken with caution as they are based on a smaller sample size. Our measurements of the flight speeds of *L. borealis* ($5.9 \pm 3.3 \text{ ms}^{-1}$ N= 5) and *L. cinereus* ($9.4 \pm 6.2 \text{ ms}^{-1}$ N = 2) are comparable to those reported using Doppler radar for these species while foraging: ($6.7 \pm 1.1 \text{ ms}^{-1}$) and ($7.7 \pm 1.1 \text{ ms}^{-1}$), respectively (Salcedo et al. 1995). At this time, I cannot determine if these flight speeds are indicative of a fly-and-forage strategy, or a consequence of low sample size.

Previous studies have suggested that migrating bats avoid flying in high winds (Cryan and Brown 2007; Baerwald and Barclay 2011). I found evidence that all species studied fly with moderate tailwind support, and are selective of when they undertake migratory movements, similar to several bird species. The presence of weather systems with appropriate tail winds should be investigated in future studies of mortality at wind energy facilities. Ground speeds were best correlated with tailwind component at surface level and 925 mb in pressure, which suggests that bats migrate somewhere between the surface and 1500 m in altitude. This is consistent with studies from Europe which found that bats migrating over the Baltic Sea flew close enough to remain in acoustic contact with the water (< 10 m). Similarly migrating *P. nathusii* were visible within 16 m of the ground (Suba 2014). More research is needed to better determine the altitude at which North American bats migrate.

5.5.3 Speed of Migration

Overall migration speed includes both periods of movement as well as stops to rest and refuel. For the first time I was able to quantify the autumn migration speed of a North American tree-bat. *L. noctivagans* traveled 133 ± 112 km per night (range 8.8 - 281 km/night). At this pace, bats would reach the Gulf of Mexico (approximately 1500 km) in 11.3 nights (range: 6.1 – 71.4 nights). The very slowest migration speed we observed (8.8 km per night) is much slower than the flight speeds we observed (50 km/h) and indicates that some bats spent several days not making migratory flights. It remains to be determined if these periods are spent foraging at stopover sites, were due to inclement weather, or were used to participate in mating activity. The much slower pace of migration than potential flight speed, which implies the use of stopovers, has also been observed in *Nyctalus noctula* (Dechmann et al. 2014). The maximal migration speed observed in this study of 281 km per day, would only be traversed if bats flew for 5.6 hours at a flight speed of 50 km/h, and shows that bats are capable of spending a large proportion of the night undertaking migratory flight. Our observed mean migration speed for *L. noctivagans* exceeds the migration speed of the common noctule (*N. noctula*; females 24.3 km per day; males 14.2 km per day)(Dechmann et al. 2014), and *P. nathusii* (55 – 75 km per day) (Hedendrom 2009; Rydell et al. 2014).

If *L. noctivagans* travel on average 133 km per day, they could cover this distance in about 2.7 hours of flying at the mean flight speeds we recorded (50 km h⁻¹). So, out of about 9.5–12.5 hours of night available at this time of year for flight or refueling, bats could spend as much as 75 % of their available active hours not making migratory movements. The theorized ratio of time to spend on migratory flight vs stopover for birds is 1:7, or about 86% of time on stopover (Hedenström and Ålerstam 1997). This is a similar proportion of time (64%) that passerine birds tracked with geolocators (two purple martins and four wood thrushes) spent at stopover (Stutchbury et al. 2009). A study of common swifts (*Apus apus*) spent even less time on stopovers, 47% in the spring and 27% in the autumn migration (Åkesson et al. 2012). *L. noctivagans* spend at least 75% of their night on non-migratory flight activities, potentially more if our estimates of flight speed also incorporate some time spent foraging or drinking.

5.5.4 Detectability

The three species varied considerably in their detectability by Motus. Several factors such as body size and flight characteristics could be responsible. The body of the bat acts as an antenna to further amplify the radio signal, and larger bats should have stronger signals (Naef-Daenzer 2005). *L. cinereus* are the largest bodied bats in this study (19 - 31 g), followed by *L. noctivagans* (8.5 - 12.5 g) and *L. borealis* (10 - 12 g). The three *L. cinereus* were frequently detected within the array space, appearing at the most towers (5-9) of any bat in this study, (*L. borealis* 1-5 and *L. noctivagans* 1-6).

Another important factor in detectability is the habitat that these bats fly through; more vegetation between the antennae and the receiving tower will decrease signal strength (Withey et al. 2001). Therefore, high, open fliers (above tower height, 6 m) are less likely to experience signal attenuation. Although bats are sometimes presumed to fly at heights similar to migrating birds, it is possible that bats migrate lower to the ground. *P. nathusii* migrate at an altitude of 11.5 m and maintain acoustic contact with the ground (Suba 2014). Similarly, bats at sea also appear to maintain acoustic contact with the ocean

(Ahlén et al. 2009). Commuting *P. kuhlii* flew closer to the ground (2.7 m), than while foraging (4.7 m) (Grodzinski et al. 2009). Lower flight altitude could also explain the low detectability of some bats in my study, because bats flying at altitudes below tower height, likely experience more signal interference from vegetation. *L. cinereus* have wings designed to favor open uncluttered habitats, which could increase the detectability of this species (Norberg and Rayner 1987). In contrast, *L. noctivagans* have wings more suitable for flying closer to vegetation (Norberg and Rayner 1987). Use of more cluttered habitats while migrating could have decreased the detectability of *L. noctivagans* and *L. borealis* as compared to *L. cinereus*. The apparent increased detectability of *L. noctivagans* in the autumn (all bats were detected on multiple towers) as compared to the spring (many bats were not detected outside of the capture site) may be partially explained by bats flying at higher altitudes in the autumn, which would increase detectability. More ground-truthing of the Motus wildlife tracking system is required to confirm the hypothesis that season affects migration height. If migratory bats fly at higher altitudes during autumn migration, they could be more likely to pass through the swept area of wind turbines, and thus be more vulnerable to collision risk in autumn than in spring. I propose that future research directly examine seasonal differences in the altitude at which migrant bats travel.

5.5.5 Summary

The Motus wildlife tracking system has proven to be an effective tool for investigating the movements of individual migrating bats. I was able to map the migratory routes of bats traveling through southwestern Ontario. Contrary to my hypothesis, I was not able to find any evidence of migratory corridors in the region. This finding makes it difficult to identify specific locales where wind energy development could proceed with lower risk to bats. Bats did travel along the shoreline of Lake Erie and wind energy facilities in this region should use some form of mitigation during both spring and autumn (e.g. increasing the wind speed at which turbines begin generating energy (e.g. Baerwald et al. 2009). Motus has also allowed us to estimate the flight speeds of North American migrating bats. This new technology holds promise for future work investigating the habits of secretive migratory species.

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CHAPTER 6

GENERAL DISCUSSION

The studies in my dissertation provide some of the first insights into the basic biology of *Lasionycteris noctivagans* during their migratory period. The main goal of my research was to determine how sex and season affect the migration of tree-bats. I addressed this goal in four ways: 1) I examined spring migration phenology and its relation to body condition; 2) I explored how sex affects the stopover behaviour of bats in the spring; 3) I investigated the torpor-assisted migration hypothesis in the spring, when females may use less torpor than males; and 4) I used the Motus wildlife tracking system to monitor the long-distance movements of migrating bats during both spring and autumn. Through several approaches I have shown that sexes manage both their time and energy differently. I have also shown that season has a substantial impact on the pace and use of energy during migration. Here I summarize and integrate my findings, discuss the potential implications for bat conservation, and I delineate paths for future research on bat migration.

6.1 SEX AND MIGRATION

6.1.1 MIGRATION TIMING

The phenology of *L. noctivagans* spring migration differed by sex. Females arrived at the stopover site earlier than males in two of the three study years. This matched my prediction of protogyny. Early arriving females give their pups a longer growing season, and so there is a reproductive advantage to early arrival for females. In contrast, males have already mated the previous autumn and are not under selection pressure to arrive early. It would be interesting to monitor breeding colonies of *L. noctivagans* to confirm that early arrival to the summering grounds advances parturition date and enhances survival of young. Early arrival could be a product of a difference in several aspects of migratory behaviour, such as their speed of travel (i.e. air speed, time spent refueling,

response to weather), latitudinal differences in overwintering sites, or the timing of their departure from the wintering grounds.

I predicted that females would have an overall more rapid pace of migration than males – either through flying more quickly, or spending briefer periods at stopover sites.

Unfortunately, there were not enough flight speed data in the spring to differentiate male and female airspeeds or migration speeds. Investigation of age and sex differences in flight speeds could be an opportunity for future research. It would be interesting to track greater numbers of male and female bats in the spring and to examine morphometrics to see if females are more adapted for rapid, efficient flight (i.e. have higher aspect ratios and/or more pointed wing tips), as has been suggested to confer earlier arrival dates in Swainson's thrushes (*Catharus ustulatus*) (Bowlin and Lank 2007).

Optimal migration theory predicts that bats will depart stopover sites when they have completed refueling. Net refueling rate is determined by both energy intake and energy expenditure. Protandry in birds can be partially determined by faster refueling, and thus briefer stopovers, by males (Seewagen et al. 2013). I found no sex difference in the length of stay at stopovers. Female bats have higher daytime thermoregulation costs than males because females use torpor for fewer hours during the day. The observed difference in torpor expression may be a product of females foraging more intensely than males, and thus spending more time at warm body temperatures to digest large meals (Matheson et al. 2010). More work is needed to determine if females forage more intensely than males while migrating.

I found that cold weather delays female, but not male migration. Female mean arrival date at the stopover site was later in colder years. The early timing of *L. noctivagans* spring migration in females makes them more susceptible to the effects of weather than males. Females travel while it is still relatively cold, and in Chapter 3, I found that cold ambient temperatures extend stopover periods and prolong migration in both sexes.

Although it is also possible that females overwinter farther north than males and so have shorter migration distances, this seems unlikely. Museum records of *L. noctivagans* collected during the winter months show no sign of sex segregation (Cryan 2003), and captures of this species in winter months include both sexes (Perry et al. 2010). Perhaps further winter observations will reveal differences in the wintering ranges of the sexes, with the current findings explained by a region of overlap.

Given that I observed no difference in the speed of migration, and there is no evidence for latitudinal segregation on the wintering grounds, it seems most likely that females depart from the wintering grounds earlier than males. A similar phenology is seen in *Myotis lucifugus* where females emerge from hibernation several weeks prior to males to begin their migration back to maternity colonies (Norquay 2013).

6.1.2 BODY COMPOSITION

During spring migration, female *L. noctivagans* had fat stores nearly double those of males in two of the three study years. This contrasts with fall migration where there is no sex difference in fat stores (McGuire et al. 2011). The larger fat stores of females (vs males) support the “reproductive hypothesis,” i.e. that fat was used after migration to fuel reproduction. This is in contrast to the “insurance hypothesis,” that proposes large fat stores help early migrants survive in poor weather. Bats may not need large fat stores as insurance against inclement weather because they are able to mitigate the costs of thermoregulation by using torpor. In the coldest study year, females bats had smaller fat stores (comparable to those of males), which suggests that cold weather experienced during migration may consume their fat stores and so impair reproduction.

6.2 SEASONAL EFFECTS ON MIGRATION

Ambient temperatures at my study site in the spring were on average 11 °C colder than in autumn. The colder spring temperatures are likely to affect both foraging opportunities (as aerial insects decline at low temperatures) and thermoregulation.

6.2.1 STOPOVER

In Chapter 3, I showed that early spring stopovers lasted for several days, while the prevailing pattern during fall migration was a stopover at Long Point for a single day (McGuire et al. 2011). Data from Chapter 5 on the migration speeds of bats suggests that bats also make stopovers of several days during autumn migration, though likely still shorter than in spring. Bats appear to spend stopovers using a combination of foraging nights when conditions permit, and torpor when cooler temperatures prevail. This suggests that bats may need to dedicate more time to refueling when insect densities are lower.

6.2.2. TORPOR

I quantified the use of daytime torpor by free-ranging spring migrants and compared it with previously published data from fall migrants (McGuire et al. 2014). All bats used torpor extensively, but its use was modulated by season, sex and temperature. Bats with larger fat stores tended to use less torpor, but this trend was not significant. The lack of significance in this relationship supports the hypothesis that this torpor use is a facultative strategy to refuel more rapidly, rather than an emergency response to a negative energy balance. Bats used more torpor at colder temperatures, but even after accounting for the effect of temperature, spring migrants used torpor for longer durations than fall migrants. I hypothesized that lower insect abundance (Doucette et al. 2011; Doty et al. 2016) and more unpredictable foraging opportunities (Munn et al. 2010) in the spring could explain seasonal differences in torpor expression because food availability is strongly linked to torpor use. Spring bats appear to compensate for lower energy availability by increasing the length of time they spend in torpor.

The use of daytime and nighttime torpor means that bats are buffered against poor conditions at stopover. This is especially useful during spring migration. Bats can wait for foraging conditions to improve with very little penalty, as was shown by the behaviour of some bats that had prolonged stopovers and remained in their roosts for several nights. The utility of torpor to wait-out poor conditions is demonstrated by observations of *L. cinereus*, which enter torpor during spring snowstorms (Willis et al. 2006). In contrast,

birds must decide whether to leave when poor refueling conditions prevail. Birds may even undertake a reverse migration when weather conditions are unfavorable (Berthold 1993).

6.2.3. MOVEMENT

Bats appeared to be more readily detected by the Motus wildlife tracking system in the autumn as compared to the spring. I hypothesized that this difference was due to an increase in flight altitude during autumn migration. Further work should be done to directly measure the altitudes of migrating bats. This could be done by tagging bats with harmonic radar transponders. If differences exist in the height at which spring and autumn migrants fly, it could in part explain the seasonal difference in mortality at wind turbines. Specifically, autumn migrants may spend more time flying within the windswept area of the turbine blades as compared to spring migrants. There is already evidence that taller turbines kill more bats, with the suggestion that turbines are sampling a higher airspace in which autumn migrants may travel (Barclay et al. 2007).

6.4 REFUELING STRATEGY

My data have demonstrated that *L. noctivagans* stop for several days during both their spring and autumn migrations. Likely these periods are used for refueling. The data presented in Chapter 4, that individuals captured later in the night have greater fat and lean mass, is highly suggestive that bats are using stopovers as refueling stages. However, the use of stopovers to refuel does not preclude the use of a mixed migration strategy that also includes a fly-and-forage component. To determine if bats use a fly-and-forage migration strategy would require the monitoring of migrating bats for feeding buzzes. Feeding buzzes are echolocation calls indicative of the last approach of prey capture, and can be used to quantify foraging activity. It is not possible to separate resident bats and those using a stopover period from bats actively migrating using stationary bat detectors.

One could attach miniaturized recorders to bats to capture their echolocation calls. This technique has been used to investigate the foraging ecology of greater mouse-tailed bats

(*Rhinopoma microphyllum*) (Cvikel et al. 2015). However, *R. microphyllum* are relatively large bodied and capable of carrying a GPS tag and small microphone weighing 3.8 g. The device is then retrieved and downloaded when the bat is recaptured in the roost. New technology is available that would use a small microphone and radio-transmitter to convey an audio signal much like that of a conventional radio station (M. Bowlin pers. comm.). If such a device were modified to also be capable of recording ultrasonic bat calls, a researcher in a car or small aircraft could chase a tree-bat long enough to determine if feeding buzzes were evenly distributed throughout a migratory flight, or if bats used brief mid-flight “stopovers” of several hours at a time to forage.

An echolocation radio-transmitter would have the added benefit of determining if bats flock during migration, as the echolocation calls of conspecifics would be audible, but quieter (Cvikel et al. 2015). Little is known about the social behaviours of bats during migration, but evidence suggests that bats do not migrate with experienced conspecifics in the way that long lived birds (e.g. swans and geese) do (Baerwald and Barclay 2016).

Ongoing work in our lab is using stable isotopes of the breath to examine the extent to which bats fuel metabolism with fat stores as compared to recently digested insects. This is an alternative way to study bats’ refueling habits and the ways in which they fuel their migratory flights.

6.5 CHALLENGES OF STUDYING MIGRATORY BATS

Throughout this research I was constantly reminded of why there is such a dearth of knowledge regarding migratory tree-bats – they are particularly difficult to capture. Many net-hours went into catching the bats in this study. I found that it was necessary to mist-net for bats throughout the entire night, from dusk until dawn. In contrast the vast majority of bat researchers open their nets from dusk until about 2:00. Further, nets of twice the usual height were often required, as tree-bats apparently fly higher than others. This capture effort was particularly necessary on the Bruce Peninsula, where after two months of intense mist-netting we caught a mere 20 tree-bats. In comparison, while mist-netting at a *Myotis* maternity colony or hibernacula, it would not be unusual to capture a

hundred bats in a single evening.

To further the study of migratory bats, we need more reliable locations at which to capture them. I propose that bird banding stations should consider operating a night crew at peak bat-capture hours – the hours after dusk and a few hours before dawn. This could provide substantial data on migration phenology, ranges, and sexual segregation of migratory tree-bats. An additional idea would be for bat researchers to compile their incidental captures of migratory tree-bats into a single database. This database would be similar to E-bird which uses public observations of songbirds to map the occurrence of species throughout the year. This bat database would build on the occurrence data mapped by Cryan (2003) to give a more detailed picture of bat migration, and perhaps even describe the response of bat migration phenology to climate change.

6.6 CONSERVATION IMPLICATIONS

Many great migrations are disappearing across the earth (Wilcove and Wikelski 2008). Migrating bats are likely also at risk due to habitat loss, wind energy development, and potentially climate change. Mortality rates are elevated during migration in birds (Sillett and Holmes 2002) and likely in bats also (Tuttle and Stevenson 1977). Therefore, the migratory period is an important time to target with conservation measures.

Migration-related mortality in gray bats (*Myotis grisescens*) was suggested to be due to “stress” or poor roost selection (Tuttle and Stevenson 1977). Availability of appropriate roosts (e.g. mature trees and snags) and foraging opportunities along the migration route may be essential for bats to successfully complete their migration. I propose that conservation of foraging habitat may be particularly important for spring migrating females, who must also prepare for reproduction. The quality of stopover habitats has been proposed to limit the populations of migrating birds (Newton 2006). Weather and foraging conditions experienced during migration will affect both survival and the time of arrival to the breeding grounds, which will in turn affect reproductive success and population recruitment. Can stopover habitat also limit the populations of bats? It seems that, depending on weather conditions, bats use stopover sites to refuel, particularly in the spring, and so they may also face similar challenges and constraints as migrating birds.

Spring migrating *M. grisescens* were twice as likely to experience mortality as fall migrants (Tuttle and Stevenson 1977). This difference in mortality could be because spring migrants have smaller fat stores than fall migrants, a pattern also seen in *L. noctivangans*. Smaller fat stores offer a smaller buffer against inclement weather and poor foraging opportunities.

6.6.1 CLIMATE CHANGE

Climate change is likely to advance the onset of spring weather. Some birds appear to be able to plastically respond to shifts in temperature on their breeding grounds by advancing their laying date (Charmantier et al. 2008), but the extent of this plasticity can be constrained by arrival date (Both and Visser 2001). Several migratory bird species are able to advance their migration timing (Gordo 2007). However, some species are unable to detect cues on the wintering grounds that conditions on the breeding grounds are advancing, causing a mismatch between migrants and their ecosystems (Jones and Cresswell 2010). Those species unable to shift their migration timing are experiencing population declines (Møller et al. 2008).

If bats are to adapt to earlier spring, they will need to either leave the wintering grounds earlier or move more rapidly. Little is known about the cues used by bats to terminate their hibernation. A large part of the emergence timing from hibernacula is likely a circannual rhythm. For tree-bats, emergence may also involve a component of local ambient temperatures. This is in contrast to bats that use cave hibernacula, as tree-bats are less buffered from local environmental conditions. Tree-bats may be plastic in their arrival timing if they are able to move more rapidly in response to warmer spring weather. Pied flycatchers (*Ficedula hypoleuca*) are able to respond to warmer temperatures along the migration route by moving more quickly (Ahola et al. 2004). Similarly, I have shown that female tree-bats already appear to shift their migration timing in response to ambient temperatures (Chapter 2). A likely mechanism for this shift in migration timing would be shortened stopover durations, which appear to be highly

temperature dependent (Chapter 3). Therefore *L. noctivagans* may be able to cope with shifting temperatures by quickening their pace of migration.

6.6.2 WIND ENERGY

Unprecedented numbers of tree-bats are killed annually at wind energy facilities, which arguably represent the largest threat to migratory tree-bat populations (Arnett et al. 2016). Wind energy development has been growing in Canada (Government of Ontario 2016). There is an urgent need to understand how to mitigate bat mortality at these wind energy facilities. I endeavoured to map the migratory routes of bats, in part so that migratory corridors could be identified and protected. I found no evidence that bats were traveling in a concentrated corridor, and instead appear to use broad-front migration (Chapter 5). This makes it difficult to identify regions in which to develop wind energy within south-western Ontario without providing mitigation for migrating bats. The shoreline of Lake Erie was used extensively during spring migration and development there should be avoided. Turbines already in place along the lakeshore should implement mitigation strategies (i.e. increasing the wind speed at which turbines begin generating power)(Baerwald et al. 2009). Most importantly, regulators should work with researchers to determine how to alter wind energy production during the short but intense migratory periods of bats.

Future work should be done to examine the use of offshore areas by bats for migratory crossings (i.e. Lake Erie). Anecdotally, migratory bats have been observed on several nights during the autumn migration period in the middle of Lake Huron between Manitoulin Island and Tobermory from the Chi-Cheemaun ferry (R. Steinecher pers. comm). Despite concerns over the impact of wind energy on bats, several offshore wind energy developments have been proposed for Lake Erie. Offshore wind energy sites are of particular concern because post monitoring surveys for mortality are not feasible. Departures from Long Point suggest that about one third of bats depart off the Long Point Peninsula and cross Lake Erie (McGuire et al. 2011). Ongoing work with the Motus network is using newly established towers on the south shore of Lake Erie to identify incidents of bats that cross the lake (L. McGuire pers. comm).

6.7 CONCLUSIONS & FUTURE DIRECTIONS

Bat migration has begun to receive more attention and continues to be an area of promising research. I have made several contributions to our understanding of their migration biology. My research has focused mostly on spring behaviour, which has been underrepresented in the literature. In Chapter 2, I found that female bats arrive at stopover earlier than males and with larger fat stores. In Chapter 3, I observed for the first time the use of multi-day stopovers by bats, and provided evidence that these stopovers are used for refueling. In Chapter 4, I discovered that the use of daytime torpor is modulated by both sex and season, to accommodate different energy budgets. Finally, in Chapter 5, I used the Motus wildlife tracking system to quantify the migration routes, flight speeds, and migration pace of bats.

There are still many unanswered questions about how bats successfully complete their migrations. Among other things, more work is needed to understand how bats orient and navigate. The Motus network is particularly well placed to help address these questions. The direction of travel in bats appears to be innate and not socially learned, as young bats on their first migration do not travel with close relatives (Baerwald and Barclay 2016). It would be interesting to translocate bats several hundred kilometers eastward or westward to southwestern Ontario to see if bats are able to compensate for displacement. It would be expected that adults, having an internal map and compass, are able to correct their direction of travel. Young bats on their first migration would be expected to travel in their programed direction.

6.8 Literature Cited

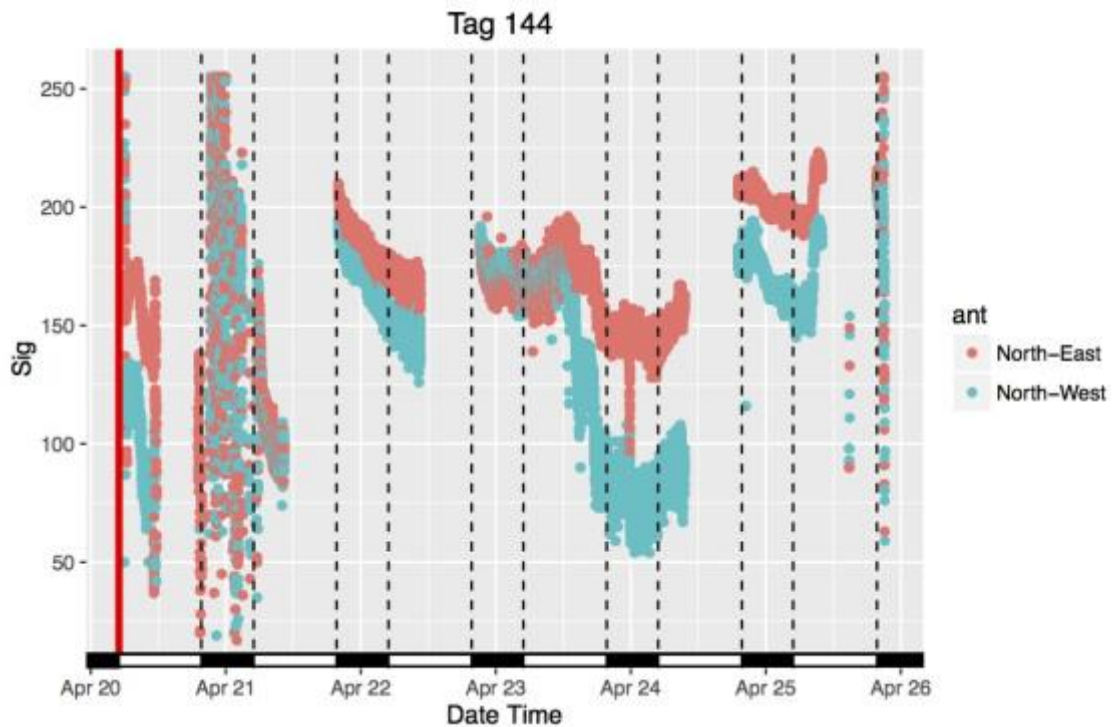
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APPENDIX A

CHAPTER 3 SUPPLEMENTARY MATERIAL



Supplementary Figure 3.1. Example of telemetry activity pattern of a bat roosting near the Old Cut receiving station. The red line denotes when the bat was tagged. Colored lines indicate signal strength on separate antennas. The bat quickly comes to roost for the daytime period, is active on the night of April 20, 2012 roosts at dawn and remains roosting until its departure at dusk on April 26, 2012. Periods of no detection during the day indicted times when the receiver was removed for manual tracking for a different project. Black bars represent periods of night, dashed lines depict sunset and sunrise.

APPENDIX B

CHAPTER 4 SUPPLEMENTARY MATERIAL

Sensorgnome deployment code

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APPENDIX C

PERMISSIONS TO REPRODUCE PUBLISHED MATERIAL

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APPENDIX D

ETHICS APPROVALS



March 25, 2010

This is the Original Approval for this protocol
A Full Protocol submission will be required in 2014

Dear Dr. Guglielmo:

Your Animal Use Protocol form entitled:
 Physiological Ecology of Migratory Birds During Stopover
 Funding Agency NSERC - Grant - 311901-05

has been approved by the University Council on Animal Care. This approval is valid from **March 25, 2010 to March 31, 2011**. The protocol number for this project is **2010-020 which replaces 2006-014 which has expired.**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
 If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 4 Years

Species	4 Year Total Numbers Estimated as Required	List All Strain(s)	Age / Weight
Songbird	22220	All native bird species as permitted by CWS and USFWS	all

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

c.c. Approval - C. Guglielmo, S. Waring, W. Lagerwerf



The University of Western Ontario
 Animal Use Subcommittee / University Council on Animal Care
 Health Sciences Centre, • London, Ontario • CANADA – N6A 5C1
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APPENDIX E

PERMITS

 Ontario Ministry of Natural Resources Ministère des Richesses naturelles		Wildlife Scientific Collector's Authorization Autorisation pour faire la collecte scientifique d'animaux sauvages		Authorization No. N° d'autorisation 1007554
This authorization is issued under Section 39 of the Fish and Wildlife Conservation Act, 1997 to: Cette autorisation est délivrée en vertu de l'article 39 de la Loi sur la protection du poisson et de la faune de 1997 à:				Local Reference No. N° de référence local 10002759
Name of Authorization holder Nom du titulaire de l'autorisation	Last Name / Nom de famille Mr. Guglielmo	First Name / Prénom Chris	Middle Name / Second Prénom G.	
Name of Business/Organization/Affiliation (if applicable) Nom de l'entreprise/l'organisme de affiliation (le cas échéant) University of Western Ontario, Department of Biology				
Mailing address of Authorization holder Adresse postale du titulaire de l'autorisation	Street Name & No./RD Rue/Rue/Get. Del./N° rue/C.P.R. R. porte restante 1151 Richmond Street North			
	City/Town/Municipality / Ville/Village/municipalité London	Province/State Province/État ON	Postal Code/Zip Code Code Postal/Zip N6A 5B7	
This authorization permits the above-named person to: Cette autorisation permet à la personne nommée ci-haut de:				
<input checked="" type="checkbox"/> Capture wildlife of the species and sex, in the numbers, and in the area set out below. Capturer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous and/or / et/ou <input type="checkbox"/> Keep game wildlife or specially protected wildlife in captivity for the purposes of education or science. Garder des animaux sauvages spécialement protégés et du gibier sauvage en captivité à des fins éducatives et scientifiques <input checked="" type="checkbox"/> Release the captured wildlife in the area of capture, if the captured wildlife is not to be removed from that area. Relâcher les animaux sauvages capturés dans la zone de capture si les animaux capturés ne doivent pas être enlevés de cette zone				
OR / OU <input type="checkbox"/> Capture and kill wildlife of the species and sex, in the numbers, and in the area set out below. Capturer et tuer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous				
Species / Espèces	Sex / Sexe	Numbers / Nombre	Location / Endroit	
<i>Lasionyx noctivagans</i>		300	Long Point Area / Cape Hurd Area	
<i>Lasiurus borealis</i>		150	Long Point Area / Cape Hurd Area	
<i>Lasiurus cinereus</i>		100	Long Point Area / Cape Hurd Area	
Yes/Oui <input type="checkbox"/> Additional list attached / Liste additionnelle ci-jointe				
Authorization Dates Dates d'autorisation	Effective Date / Date d'entrée en vigueur (YYYY-MM-DD) 2012-03-15	Expiry Date / Date d'expiration (YYYY-MM-DD) 2012-11-30		
Authorization conditions Conditions de l'autorisation This authorization is subject to the conditions contained in Schedule A if included / Cette autorisation doit respecter les conditions de l'annexe A si celle-ci est jointe. Yes/Oui: <input checked="" type="checkbox"/> No/Non: <input type="checkbox"/> Schedule A included / Annexe A ci-jointe				
Authorized by (please print) Autorisé par (veuillez écrire en caractères d'imprimerie) Sherry Pineo		Signature of Authorizer / Signature de la personne chargée d'autoriser 		Date of issue / Date de délivrance (YYYY-MM-DD) 2012-03-23
Signature of Authorization holder / Signature 		Date (YYYY-MM-DD) 2012-03-23		

Personal information contained on this form is collected under the authority of the Fish and Wildlife Conservation Act, 1997 and will be used for the purpose of licensing, identification, enforcement, resource management and customer service surveys. Please direct further inquiries to the District Manager of the MNR issuing district.
 Les renseignements personnels dans ce formulaire sont recueillis conformément à la Loi sur la protection du poisson et de la faune, 1997, et ils seront utilisés aux fins de délivrance de permis, d'identification, d'application des règlements, de gestion des ressources et de sondage sur les services à la clientèle. Veuillez communiquer avec le chef du district du MNR qui délivre le permis si vous avez des questions.



Ministry of
Natural Resources
Ministère des
Richesses naturelles

Wildlife Scientific Collector's Authorization

Autorisation pour faire la collecte scientifique d'animaux sauvages

This authorization is issued under Section 39 of the Fish and Wildlife Conservation Act, 1997 to:
Cette autorisation est délivrée en vertu de l'article 39 de la Loi sur la protection du poisson et de la faune de
1997 à:

Authorization No. N° d'autorisation	1073085
Local Reference No. N° de référence local	
Issuer Account No. N° de compte du délivreur de permis	10002759

Name of Authorization holder	Last Name / Nom de famille Mr. Guglielmo	First Name / Prénom Christopher	Middle Name / Second Prénom G
Name of Business/Organization/Affiliation (if applicable) Nom de l'entreprise/de l'organisme/de l'affiliation (le cas échéant)	Department of Biology, University of Western Ontario		

Mailing address of Authorization holder	Street Name & No./RD Bou/Rue/Cen. Del / N° rue/C.P./R.R./poste restante 1151 Richmond Street North		
Address postale du titulaire de l'autorisation	City/Town/Municipality / Ville/Village/municipalité London	Province/State ON	Postal Code/Zip Code Postal/Cp N6A 5B7

This authorization permits the above-named person to:
Cette autorisation permet à la personne nommée ci-haut de:

- ☒ Capture wildlife of the species and sex, in the numbers, and in the area set out below.
Capturer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous
and/or / et/ou:
- ☐ Keep game wildlife or specially protected wildlife in captivity for the purposes of education or science.
Garder des animaux sauvages spécialement protégés et du gibier sauvage en captivité à des fins éducatives et scientifiques
- ☒ Release the captured wildlife in the area of capture, if the captured wildlife is not to be removed from that area.
Remettre en liberté les animaux sauvages capturés dans la zone de capture si les animaux capturés ne doivent pas être enlevés de cette zone

OR / OU

- ☐ Capture and kill wildlife of the species and sex, in the numbers, and in the area set out below.
Capturer et tuer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous

Species / Espèce	Sex / Sexe	Numbers / Nombre	Location / Endroit
Lanius borealis			Long Point Area
Lanius borealis			Long Point Area
Lanius borealis			Long Point Area

Yes/Oui

☐ Additional list attached / Liste additionnelle ci-jointe

Authorization Date Date d'autorisation	Effective Date / Date d'entrée en vigueur (YYYY-MM-DD) 2013-04-01	Expiry Date / Date d'expiration (YYYY-MM-DD) 2013-06-30
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Authorization conditions: This authorization is subject to the conditions contained in Schedule A if included / Cette autorisation doit respecter les conditions de l'annexe A si celle-ci est jointe.

Conditions de l'autorisation: Yes/Oui: ☒ No/Non: ☐ Schedule A included / Annexe A ci-jointe

Authorized by (please print) Autorisé par (s'il vous plaît écrire en caractères d'imprimerie): Dave Richards	Signature of Authorizer / Signature de la personne chargée d'autoriser 	Date of issue / Date de délivrance (YYYY-MM-DD) 2013-04-03
Signature 		Date (YYYY-MM-DD) 2013-04-03

Personal information on this form collected under the authority of the Fish and Wildlife Conservation Act, 1997 and will be used for the purpose of licensing, identification, enforcement, resource management and customer service surveys. Please direct further inquiries to the District Manager of the MNR issuing license.
Les renseignements personnels dans ce formulaire sont recueillis conformément à la Loi sur la protection du poisson et de la faune, 1997, et ils seront utilisés aux fins de délivrance de permis, d'identification, d'application des règlements, de gestion des ressources et de sondage sur les services à la clientèle. Veuillez communiquer avec le chef du district du MNR qui délivre le permis si vous avez des questions.

Document 00000



Ministry of
Natural Resources
Ministère des
Richesses naturelles

Wildlife Scientific Collector's Authorization

Autorisation pour faire la collecte scientifique d'animaux sauvages

This authorization is issued under Section 39 of the Fish and Wildlife Conservation Act, 1997 to:
Cette autorisation est délivrée en vertu de l'article 39 de la Loi sur la protection du poisson et de la faune de
1997 à:

Authorization No. N° d'autorisation	1076439
Local Reference No. N° de référence locale	
Issuer Account No. N° de compte du délivreur de permis	10002549

Name of Authorization holder	Last Name / Nom de famille Mr. Guglielmo	First Name / Prénom Christopher	Middle Name / Second Prénom G.
Name of Business/Organization (if applicable) Nom de l'entreprise/de l'organisme de l'autorisation (le cas échéant)	University of Western Ontario		
Mailing address of Authorization holder	Street Name & No./RD, Bou/Rd/Gen. Del./MP, rue/C.P./R.R., poste restante 1151 Richmond St.		
Address postale du titulaire de l'autorisation	City/Town/Municipality / Ville/Village/municipalité London	Province/State Provinces/États ON	Postal Code/Zip Code Code Postal/Zip N6A 5B7

This authorization permits the above-named person to:
Cette autorisation permet à la personne nommée ci-haut de:

- ☒ Capture wildlife of the species and sex, in the numbers, and in the area set out below.
Capturer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous
and/or / et/ou
- ☐ Keep game wildlife or specially protected wildlife in captivity for the purposes of education or science.
Garder des animaux sauvages spécialement protégés et du gibier sauvage en captivité à des fins éducatives et scientifiques
- ☒ Release the captured wildlife in the area of capture. If the captured wildlife is not to be removed from that area.
Relâcher en liberté les animaux sauvages capturés dans la zone de capture si les animaux capturés ne doivent pas être enlevés de cette zone

OR / OU

- ☐ Capture and kill wildlife of the species and sex, in the numbers, and in the area set out below.
Capturer et tuer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous

Species / Espèces	Sex / Sexe	Numbers / Nombre	Location / Endroit
Lasiurus noctivagans		250	Long Point, Bruce Peninsula
Lasiurus borealis		100	Long Point, Bruce Peninsula
Lasiurus cinereus		100	Long Point, Bruce Peninsula

Yes/oui

☐ Additional list attached / Liste additionnelle ci-jointe

Authorization Dates Date d'autorisation	Effective Date / Date d'entrée en vigueur (YYYY-MM-DD) 2014-04-04	Expiry Date / Date d'expiration (YYYY-MM-DD) 2014-12-31
Authorization conditions Conditions de l'autorisation	The authorization is subject to the conditions contained in Schedule A if included. / Cette autorisation doit respecter les conditions de l'annexe A si celle-ci est jointe. Yes/oui: <input checked="" type="checkbox"/> No/non: <input type="checkbox"/> Schedule A included / Annexe A ci-jointe	
Authorized by (please print) Autorisé par (veuillez écrire en caractères d'imprimerie) Brad Connor	Signature of Authorizer / Signature de la personne chargée d'autoriser 	
Signature of Authorization holder / Signature du titulaire de l'autorisation 	Date of Issue / Date de délivrance (YYYY-MM-DD) 2014-04-04	
	Date (YYYY-MM-DD) 2014-04-04	

Personal information contained on this form is collected under the authority of the Fish and Wildlife Conservation Act, 1997 and will be used for the purpose of licensing, identification, enforcement, resource management and customer service surveys. Please direct further inquiries to the District Manager of the MNR issuing permit.

Les renseignements personnels dans ce formulaire sont recueillis conformément à la Loi sur la protection du poisson et de la faune, 1997, et ils seront utilisés aux fins de délivrance de permis, d'identification, d'applications des règlements, de gestion des ressources et de sondages sur les services à la clientèle. Veuillez communiquer avec le chef du district du MNR qui délivre le permis si vous avez des questions.

CURRICULUM VITAE

KRISTIN A. JONASSON

ACADEMIC TRAINING

Ph.D. *University of Western Ontario, Canada* **Current Position**

“Energy Balance & Movement Ecology of Bat Migration”

Advisor: Dr. Christopher G. Guglielmo

M.Sc. *University of Winnipeg, Canada* Jun 2011

“Hibernation Energetics of Little Brown Bats”

Advisor: Dr. Craig K.R. Willis

B.Sc. (Honors first class) Zoology, *University of Calgary, Canada* May 2008

“Characterization and Distribution of Gekkoinid Axial Skeletal Tissues”

Advisor: Dr. Anthony P. Russell

SCHOLARSHIPS & AWARDS

NSERC – CGS D Graduate fellow 2012-2015

Top-ranked applicants of the CGS competition

Governor General’s Academic Gold Medal 2011

Awarded to the highest ranked graduating student

University of Winnipeg Graduate Student Colloquium Best Presentation 2010

NSERC – CGS M Graduate fellow 2009-2010

Top-ranked applicants of the CGS competition

Manitoba Graduate Scholarship 2008-2009

GRANTS

Species at Risk Research Fund Ontario (\$ 20,750) – 2014

PI: Dr. Y. Morbey

Co-PIs: Dr. C.G. Guglielmo & K.A Jonasson

University of Western Ontario Graduate Studies Travel Grant (\$ 500) – 2014

Bat Conservation International Student Research Grant (\$ 3,350) – 2012-2013

University of Winnipeg Graduate Studies Travel Grant (\$ 750) – 2009

University of Winnipeg Graduate Studies Travel Grant (\$ 750) – 2008

Bat Conservation International Student Research Grant (\$3,500) – 2008-2009

SERVICE AND OUTREACH

Peer Reviewer of manuscripts in *Northeastern Naturalist*, *Ibis*

Biological Sciences Graduate Student Representative, *University of Winnipeg 2008-2010*
MORE DETAIL.

PEER-REVIEWED PUBLICATIONS

6 peer reviewed publications **1** submitted publication **8** international conference presentations

Submitted

- (1) Czenze, Z. J., **Jonasson, K.A.**, and Willis, C.K.R. (No. 16154). Thrifty females, frisky males: winter energetics of hibernating bats in a cold climate. *Physiological and Biochemical Zoology*

Published

- (6) **Jonasson, K.A.**, and Guglielmo C.G.G. (2016). Sex differences in spring migration timing and body composition of silver-haired bats *Lasionycteris noctivagans*. *Journal of Mammalogy*
- (5) McGuire L.P., **Jonasson, K.A.**, and Guglielmo C.G.G. (2014). Bats on a budget: torpor-assisted migration saves time and energy. *PloS One* **9**:12, e115724
- (4) **Jonasson, K.A.** and Willis, C. K. R. (2012). Hibernation energetics of free-ranging, little brown bats. *Journal of Experimental biology*. **215**: 2141-2149
Featured in “Inside JEB”
- (3) **Jonasson, K.A.**, Russell, A.P. and Vickaryous, M.K. (2012). Histology and histochemistry of the gekkotan notochord and their bearing on the development of notochordal cartilage and the origin of cartilage in chordates. *Journal of Morphology*. **273**: 596–603
- (2) **Jonasson, K.A.**, and Willis, C. K. R. (2011). Changes in body condition of hibernating bats support the thrifty female hypothesis and predict consequences for populations with white-nose syndrome. *PLoS ONE* **6**, e21061.
- (1) **Jonasson, K.A.**, Timonin, M. E., Norquay, K., Menzies, A. K., Dubois, J. and Willis, C. K. R. (2010). Case Study: a little brown bat (*Myotis lucifugus*) survives in the wild with only one foot. *Journal of Wildlife Rehabilitation* **30**, 7-9.

SELECTED CONFERENCE PRESENTATIONS

- (11) **Jonasson K.A.** and Guglielmo, C.G.G. Flight tracks of migrating tree-bats: a comparison of spring and autumn movements Talk presented at The 17th International Bat Research Conference (Durban, South Africa) Aug 2016.
- (10) **Jonasson K.A.** and Guglielmo, C.G.G. Spring migration strategies of male and female silver-haired bats (*Lasionycteris noctivagans*). **Hoar award finalist.** Talk presented at The Canadian Society of Zoologists (London, Canada) May 2016
- (9) **Jonasson K.A.** and Guglielmo, C.G.G. Migration timing and body composition of silver-haired bats (*Lasionycteris noctivagans*). Talk presented at The 44th North American Symposium on Bat Research (Monterey, USA) Oct 2015
- (8) **Jonasson K.A.** and Guglielmo, C.G.G. Stopover ecology of spring migrating silver-haired bats. **Awarded 3rd best talk**, presented at Berlin Bat Meeting: Movement Ecology (Berlin, Germany) Mar 2015
- (7) **Jonasson K.A.** and Guglielmo, C.G.G. Sex differences in torpor use of spring migrating silver-haired bats. Talk presented at Society for Integrative Comparative Biology (Palm Beach, USA) Jan 2015
- (6) **Jonasson K.A.** and Guglielmo, C.G.G. Migratory Movements of Tree Bats Across Southwestern Ontario. Poster presented at The 43rd North American Symposium on Bat Research (Albany, USA) Oct 2015
- (5) **Jonasson K.A.** and Guglielmo, C.G.G. Sex differences in stopover durations of spring migrating silver-haired bats. Talk presented at Canadian Society of Zoologists (Guelph, Canada)
- (4) **Jonasson K.A.** and Guglielmo, C.G.G. Stopover durations of spring migrating silver-haired bats. Talk presented at The 42nd North American Symposium on Bat Research (San Juan, Puerto Rico)
- (3) **Jonasson K.A.** and Willis, C.K.R. Variation in Hibernation Patterns of Free-ranging, Little Brown Bats. Talk presented at The 41st North American Symposium on Bat Research (Toronto, Canada)
- (2) **Jonasson K.A.** and Willis, C.K.R. Optimization of Hibernation in *Myotis lucifugus* - the Thrifty Female Hypothesis. Talk presented at The 40th North American Symposium on Bat Research (Denver, USA)
- (1) **Jonasson K.A.** – The Sex Effect: Hibernation Energetics in Little Brown Bats (*Myotis lucifugus*). Talk presented at Prairie University Biology Symposium (Brandon, Canada)